

# HANDBOOK OF THE BIRDS OF THE WORLD

## Volume 6 Mousebirds to Hornbills



  
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Blue-naped Mousebird (*Urocolius macrourus*)  
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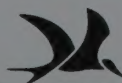
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## Volume 6

Mousebirds *to* Hornbills

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Barcelona

Recommended citation:  
**del Hoyo, J., Elliott, A. & Sargatal, J.** eds. (2001). *Handbook of the Birds of the World*. Vol. 6. Mousebirds to Hornbills.  
Lynx Edicions, Barcelona.

Citation to individual contributions recommended in the following format:  
**de Juana, E.** (2001). Family Coliidae (Mousebirds). Pp. 60-77 in: del Hoyo, J., Elliott, A. & Sargatal, J. eds. (2001).  
*Handbook of the Birds of the World*. Vol. 6. Mousebirds to Hornbills. Lynx Edicions, Barcelona.

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Printed on paper manufactured by Sappi in a totally acid-free watersystem.

Colour reproductions by *Edifilm, S.A.* Barcelona  
Printed and bound in Barcelona by *Grafos, S.A. Arte sobre papel*  
Dipòsit Legal: B-350-2001  
ISBN: 84-87334-30X



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## Foreword

### Avian Bioacoustics

*A tribute to Luis Baptista<sup>1</sup>*

*"... the Canyon Wren comes first on my list; to hear its song in the desert or on the desert islands of the Sea of Cortez is ... Ecstasy; it is one of the most joyous sounds I can think of ... a second favorite of mine is the Swainson's Thrush which occurs all around my house. There is even one in my garden, which is surrounded by tall willows. This bird's song conveys to me a sense of peace and as I hear its song fade away I think of Montserrat singing her aria from Puccini's Turandot, and her heavenly voice gradually, ever so gradually, fades into silence. I feel then that I had died and gone to Heaven."*

– Luis Baptista, 30 December 1999,  
responding to a question about his favorite bird songs

*The pleasure we feel listening to birds makes me wonder if the right kind of analysis would show that birdsongs share underlying principles of tonality and organization with music.*

Peter Marler,  
University of California, Davis, USA

*Do humans and birds, especially those with pleasing and expressive songs, share a deep biological appreciation for music and musicality, and is it ultimately traceable to our respective genes.*

Paul C. Mundinger,  
Queens College, New York, USA

Birds are delightfully noisy animals, and we humans have appreciated their sounds in so many ways. Poets have immortalized the songs of Old World birds like nightingales and skylarks, for example, just as songs of thrushes and wrens have enchanted New World naturalists. This aesthetic beauty of bird song was championed by Charles Hartshorne (1973), who compared the musical abilities of birds throughout the world. This music in bird song (Elliott 1999) is heard and celebrated by many of us, as it was by Mozart himself (West & King 1990). We humans also incorporate bird song into our own music, the relationship between music and bird song being a special interest of the late Luis Baptista (Dreifus 2000). Songs are appreciated in other ways, too, such as by those who love to watch and identify birds; birders value bird sounds not only for their outright aesthetic appeal but also as an aid in identifying different species. Rare is the person who could not appreciate the beauty of a nightingale's songs, who could not marvel at the vocal vigor with which birds greet the dawn, or who could not be enchanted by some of the most exquisite sounds of our natural world.

Given all this appeal, then, it is no wonder that inquisitive humans began asking questions about these sounds. Why does the nightingale sing in the first place, and why are the songs so beautiful? Who is listening, and for what purpose? Does he seek to impress other males, or perhaps females, or perhaps himself? As we hear him deliver song after song, we ask why successive songs are so different, and how many different songs he can sing. And just how does he make those sounds? What specialized voice box or neural or hormonal machinery might he have that enables him to produce such exquisite songs? Over the lifetime of this individual, how did he come to sing this particular way? How much of his song and singing style is dictated by genes he has inherited, and how much must be learned from his elders, as a cultural tradition? Over the lifetime of this particular species, how did this behavior evolve? How did the ancestral nightingale sing, and how or why has the behavior of this lineage changed? We notice simpler vocalizations from this nightingale, too, as he interacts at close range with other nightingales, and we repeat all of our questions as

*Scarlet-rumped Trogons*  
(*Harpactes duvaucelii*) in their  
Bornean rainforest habitat.

[Painting by Albert Earl Gilbert]

<sup>1</sup> Luis Baptista produced a draft of this foreword before his untimely death in June 2000. At the request of HBW editors Andy and Josep, I completed the task. It was a sad labor, but a labor of love. I remember well the day Luis and I met back in the spring of 1971, at Berkeley: his house was full of birds, as was his heart, and his affection for his White-crowns was especially contagious. His last communication with me in late 1999 (see above) is vintage Luis, as he told of his love for singing wrens and thrushes. Luis, I share with the world your last thoughts sent to me, so that all your friends and colleagues will know where to find you. — Don Kroodsmas



we ponder how he uses his entire vocabulary. Indeed, questions abound about every possible aspect of what we hear.

Such questions are the province of avian bioacoustics, the study of how birds use sound to communicate with each other. No question is too small, no question too big. Some questions are easily answered, such as how many different songs a nightingale sings (up to 200 for the Common Nightingale *Luscinia megarhynchos*—see Todt & Hultsch 1996). Answers to other questions, such as for whom the male sings, are more elusive. Given increasing interest in avian bioacoustics, the primary literature grows exponentially, as do attempts to review, synthesize, and integrate the facts and ideas with broader issues of how all animals communicate. Our growing knowledge is revealed in volumes appearing during the 1960's (Thorpe 1961; Armstrong 1963; Greenewalt 1968; Hinde 1969), 1970's (Thielcke 1970b; Hartshorne 1973; Jellis 1977; Sebeok 1977; Smith 1977), 1980's (Kroodsma & Miller 1982a, 1982b), and especially the 1990's (McGregor 1992; Catchpole & Slater 1995; Hauser 1996; Kroodsma & Miller 1996; Bradbury & Vehrencamp 1998; Hopp *et al.* 1998; Hauser & Konishi 1999; Pepperberg 1999).

In this foreword, we<sup>2</sup> offer our personal perspective on the field of avian bioacoustics, which has been the focus of our passion for a combined 70 or so years. As a tribute to the late Luis Baptista, this personal perspective is supplemented by questions submitted by a number of colleagues who were asked "To what question in avian bioacoustics would you (perhaps most) like an answer?" The questions are placed appropriately in the margins of the text, and are intended to reveal the diverse research interests of avian bioacousticians and some of the great unknown questions that drive them. In the following text, we begin with a brief discussion of the technological advances that have helped enable the rapid growth in the field. Then, in turn, we discuss how birds produce and perceive their sounds, how an individual develops its vocalizations, what the functions of those vocalizations are, and a discussion of the evolution of sound. We conclude with a look forward, discussing conservation, the increasing importance of sound archives, and the limitless possibilities for future study.

## Bioacousticians and their machines

Although all modern scientists use an increasing array of gear, the study of bird sounds did not await a technological revolution. In 1773, for example, Barrington (1773: 249) presented to the Royal Society his experiments and observations on "a subject that hath never before been scientifically treated". Barrington had reared young birds of many species in his home, and ramifications of his discoveries continue to be the focus of current studies. Barrington described, for example, how young birds must practise their songs, much like "the imperfect endeavour in a child to babble" (p. 250). After 10 to 11 months, the song becomes "fixed, and is scarcely ever altered" (p. 251). "Notes in birds are no more innate, than language is in man" (p. 252), as Barrington showed that young songbirds could routinely learn songs of other species. How young birds developed their songs was studied by others, too, such as Scott (1901) in the New World. Other "research" had been done over the past several centuries, too, as bird-fanciers, with nothing but their unaided ears and aesthetic tastes, conducted a marvellous experiment in artificial selection, showing that certain qualities of canary (Common Canary *Serinus canaria*) songs can breed true in different lineages (Güttinger 1985; Mundinger 1995).

In the field, too, much was learned with patience, hard work, and a good ear. Saunders (1929) developed a system of note-taking that allowed him to compare singing behaviors of a great diversity of species. The fine details in songs of Song Sparrows (*Melospiza melodia*) were appreciated by Margaret Morse Nice (1943). She learned that males in her Ohio (USA) population had repertoires of up to 10 or so different songs, and she studied how the males used those songs in different contexts. She was fascinated by how young birds acquired their songs, clearly learning some of the details from certain adults in the population. Another early study was that by Craig (1943), who studied the singing behavior of Eastern Wood Pewees (*Contopus virens*), describing important differences between dawn and daytime singing, a topic that persists as crucial for understanding the function of song (see below). Even today, much can still be learned by keen observers who simply watch and listen to birds carefully; no machines are needed for so many kinds of studies, such as determining the contexts in which birds use certain

*Why do we perceive bird song as beautiful? Do we share with birds an appreciation for this beauty, and has an aesthetic sense influenced evolution of beautiful songs among birds?*

Drew King and Meredith West,  
Indiana University, Bloomington, USA

*Why do birds SING, as opposed to croak or yell or something?*

Andy Horn, Dalhousie University,  
Halifax, Nova Scotia, Canada

<sup>2</sup> When I started revising Luis' foreword, using "we" felt awkward, but I soon began to feel as if Luis and I were conversing again. So he and I will use "we" as we write, and ask the reader to join us in thinking about birds and their sounds (though at times it will still feel awkward, as in the very next sentence of the text).





Figure 1. Luis Baptista in the field, on Socorro Island, where he worked to re-establish a population of the Socorro Dove (*Zenaida graysoni*) and to help preserve the island's ecosystem and its endemic birds. In Luis' left hand is a miniature parabolic reflector, with a microphone mounted at the focal point, and cradled in his right is a cassette tape recorder. Also around his neck are the essential binoculars, camera, and compass.

[Photo by Helen Horblit]

Figure 2. Seeing a bird song in the form of a sonagram and a waveform helps us hear better, too. A sonagram is a frequency-time graph, with frequency on the vertical axis (in kiloHertz, or kHz, which is thousands of cycles/second), time on the horizontal. A pure whistle, unmodulated in frequency, is a horizontal line on the sonagram; a noisy sound, such as the drumming of a woodpecker, is a broad-band vertical mark. On the sonagram, amplitude is coded in the relative blackness, but a better picture of amplitude versus time is displayed by a waveform. (A) A sonagram shows two simple whistles in the "fee-bee" song of the North American Black-capped Chickadee (*Parus atricapillus*); the first whistle is a little higher in frequency than the second whistle, and the entire 2-note song occurs in less than a second. (B) A waveform shows better the relative loudness of the two whistled notes. The "bee" actually consists of two parts, with an amplitude drop between them, making "fee-bee-ee" a better rendition of the song than "fee-bee" and reflecting the 3-part structure of the song. (C) Drumming of a Black-backed Woodpecker (*Picoides arcticus*), showing broad-band noise for each strike of the drumming surface (from Peterson 1991).

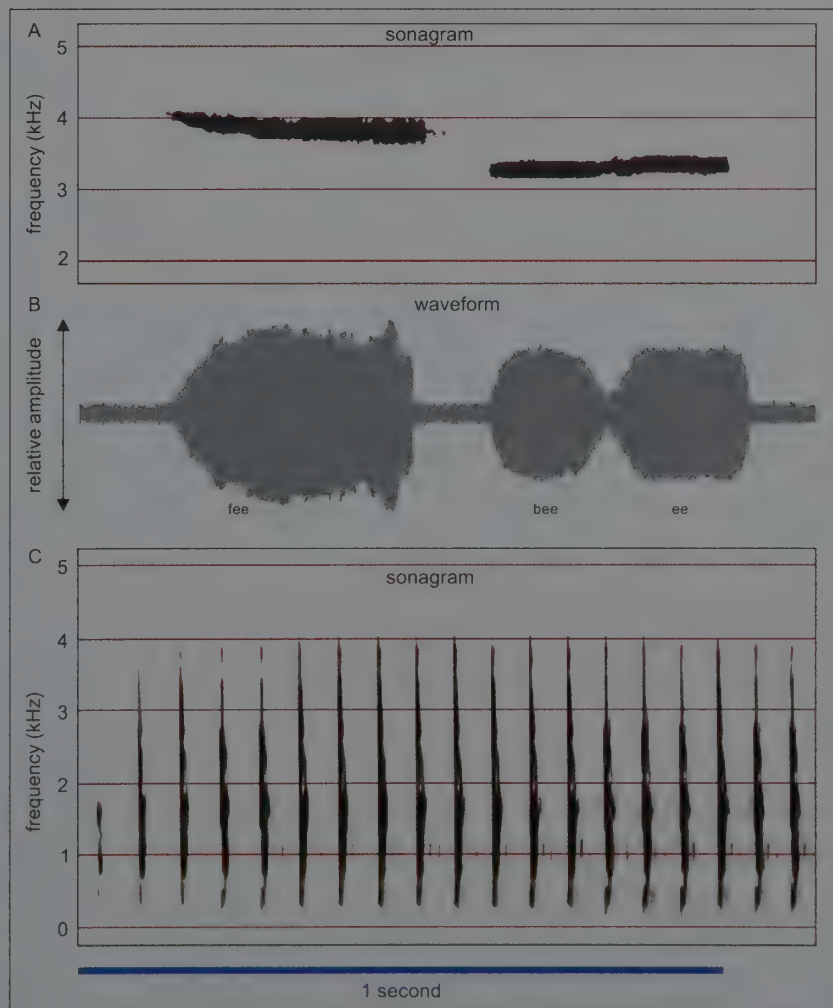
The "bee" actually consists of two parts, with an amplitude drop between them, making "fee-bee-ee" a better rendition of the song than "fee-bee" and reflecting the 3-part structure of the song. (C) Drumming of a Black-backed Woodpecker (*Picoides arcticus*), showing broad-band noise for each strike of the drumming surface (from Peterson 1991).

vocalizations, or discovering examples of interspecific vocal learning in nature, or mapping geographic song variants that are distinctive to our ears.

Although these studies achieved considerable understanding of birds and their sounds, further advances would require the ability to dissect and analyze the sounds. Perhaps the most important breakthrough for the field of bioacoustics was the invention of the magnetic tape recorder by German scientists during World War II (Baptista & Gaunt 1994). The tape recorder, along with improved microphones and parabolic reflectors (Kellogg 1962), enabled sounds to be "captured" and stored for later analysis (see also Wickstrom 1982). Current advice on both recording equipment and techniques can be found at the web site of the Library of Natural Sounds at Cornell University ([birds.cornell.edu/LNS/](http://birds.cornell.edu/LNS/)).

Especially crucial was the invention of the sound spectrograph machine. This device, developed by The Bell Laboratories prior to World War II, converts recorded sounds to pictures of frequency versus time, enabling scientists to measure the details of songs and produce objective, rather than anecdotal, descriptions of bird repertoires (e.g. Borror & Reese 1953; Collias 1991). Complementing sonagrams are waveforms, which graph amplitude versus time, and amplitude spectra, which graph amplitude versus frequency. Although these visual representations of sounds look like "hen scratchings" to the uninitiated, a little familiarity with how to read them reveals how useful they can be (see Fig. 2).

Improvements in these basic instruments have helped revolutionize the study of bird (and other animal) sounds. The original sound spectrograph took what seemed an eternity (actually only several minutes) to produce a sonagram of a few seconds' duration, but the continuous spectrum analyzer could capture sounds in real time (Hopkins *et al.* 1974), so that exciting songsters with large and varied song repertoires could be studied. We learned of Northern Mockingbirds (*Mimus polyglottos*), for example, that males have a hundred or so different songs, and that repertoire size may influence reproductive success (Howard 1974). It was downright exhilarating to graph hours of a male Brown Thrasher's (*Toxostoma rufum*) effort and discover that



he could sing well over a thousand, and perhaps 2000 different songs (Kroodsma & Parker 1977); with the advent of the continuous spectrum analyzer, some of us felt like kids in a candy store, eager to deploy this new machine to help understand what these vocal virtuosos were doing.

More recently, advances in computer technology have provided special programs dedicated to sound analyses, e.g. SIGNAL from Engineering Design (Beeman 1996) and CANARY from the Cornell Laboratory of Ornithology (Charif *et al.* 1995), and a variety of other excellent programs. Digital technology (e.g. see Beeman 1998; Clements 1998) now enables animal sounds to be acquired, analyzed, and even synthesized with an ease unimagined only a few years ago, though a few pitfalls do await those who fail to understand some of the basics of how this technology works (e.g. see Stoddard 1998 for the importance of understanding how to use filters for animal sounds). Computers now also allow us to interact with birds in a more realistic fashion (Dabelsteen 1992), as we can now respond to a bird with any sound that had been stored in the computer's memory.

## *How birds produce and perceive sounds*

Sounds that birds use in communication can be produced either by "instruments", such as special feather structures, or by the vocal organ, the syrinx. The signal must then be transmitted through a medium (usually air) to the recipient, which must then extract relevant information in the signal from ambient noise. How the nervous system controls both production and perception of the signal, and how the environment influences signal transmission are topics in which exciting advances are being made.

### **1) Producing instrumental sounds**

Specialized feather structures that produce sounds have evolved in many unrelated lines of birds (for review, see Prum 1998). Perhaps the most well-known instrumentalist is the Common Snipe (*Gallinago gallinago*; Fig. 3). Its outer tail feathers are stiffer because they are held together by more barbule hooklets than the other rectrices. During courtship the male flies high into the sky and then dives earthward with tail spread wide. The tail produces a pulsed humming sound, rendered as "wu-wu-wu-wu... ", each "wu" corresponding to one wing beat as air is forced past these specialized feathers. This is a "long delicate eerie sound. It begins softly and increases in loudness and frequency as a dive progresses, reaching a crescendo just before a dive ends" (Miller 1996, p. 243). Proof that the humming is produced by the outermost rectrices comes from the experiments of Reddig (1978). He placed these specialized rectrices in a wind-tunnel and showed with spectrograms that sounds emanating from the tunnel were similar spectrally to those recorded during courtship in the wild.

Another instrumentalist is the male Broad-tailed Hummingbird (*Selasphorus platycercus*), which has narrow outermost primaries that emit shrill whistles as the male performs territorial flight displays. This flight display can be silenced if the notch in the spread narrow primaries is blocked with glue. Birds then become less aggressive and lose their territories to other males. Removing the glue with acetone restores the wing whistles and with these the performer's territorial rights (Miller & Inouye 1983).

Evidence from another species, the Flappet Lark (*Mirafra cinnamomea*), reveals that some instrumental sounds are learned from adults. By clapping their wings during aerial displays, males produce trains of snapping noises. Neighbors have more similar flapping rhythms than do non-neighbors, thus revealing that these local rhythms are apparently learned by young birds that enter a given breeding neighborhood (Payne 1978a), much like young songbirds of some species learn the local song dialect in their breeding neighborhood (see below).

At least one species produces its instrumental sounds with a "manufactured tool". During courtship, the male Palm Cockatoo (*Probosciger aterrimus*) breaks a branch from a tree and shapes it into a "drum stick". As part of his courtship, he then holds the stick with his foot and drums on a hollow log with a preferred resonance (Wood 1984).

A large group of master instrumentalists, of course, is the woodpeckers. They drum on selected trees that seem to maximize resonance and sound transmission (Eberhardt 1997), with different species in a community typically distinguishable by unique rhythms. In North America, for example, the drumming sounds of the closely related and phenotypically similar Downy and Hairy Woodpeckers (*Picoides pubescens* and *P. villosus*) are distinctive, as are those of the Nuttall's and Ladder-backed Woodpeckers





Figure 3: Two avian instrumentalists.

(a) During display dives, air from the wings flows over the extended, outermost tail feathers of the male Common Snipe, producing a humming "wu-wu-wu-wu..." (from Cramp 1988).

(b) The narrow outermost primaries of a male American Woodcock (*Scolopax minor*) "twitter" melodiously during display flights over the breeding grounds (from Keppie & Whiting 1994).

[Figure by Francesc Jutglar]

(*P. nuttalli* and *P. scalaris*—Stark *et al.* 1998). Further study of woodpecker drumming may reveal community-wide patterns of divergence or convergence. Exactly how carefully woodpeckers choose their drumming substrates is open to study, as suggested by the observation that a male Williamson's Sapsucker (*Sphyrapicus thyroideus*) produced sounds of seven different pitches and tonal qualities by drumming on seven different sites situated on two different snags (Baptista & Keister 2000). It even seemed that he was matching his neighbor's drumming with a drum of the same pitch at a selected site, much like neighboring territorial songbirds use identical songs in their repertoires when they interact (i.e. matched countersinging—see Beecher *et al.* 2000 for review).

## 2) Producing vocal sounds

The vocal sounds of birds originate in the syrinx, which consists of paired vocal organs near the junction of the two primary bronchi and the trachea (Fig. 4; for recent reviews, see Gaunt & Nowicki 1998; Suthers 1999a). The syringes of all birds have at least one pair of rather membranous walls that can be distended into the airstream in the bronchi (i.e. internal tympaniform membranes), and others have denser but still flexible pads that can also extend into the airstream (e.g. internal and external labia). These membranes and pads are tightened or relaxed by external muscles (e.g. the sternotrachealis) that can change the length of the trachea, thereby controlling how much these membranes or pads vibrate in the airstream. Finer control is accomplished by the more complex syringes, as in songbirds, which have additional muscles (internal musculature) that are believed to control the membranes and tissues of the syrinx directly. Although all birds except New World vultures have syringes, the diversity in syringeal structure among avian orders is considerable (King 1989), and syringeal complexity is not obviously correlated with the complexity of sounds produced (Baptista & Trail 1992).

One of the most fascinating consequences of the paired syringeal morphology is that birds can produce their own "internal duet". The first convincing demonstration of this two-voice theory was by Greenewalt (1968), who based his conclusions on careful study of spectrograms and waveforms of the sounds that the birds produced. Conclusive proof of this two-voice ability in birds awaited the development of micro-techniques that allowed measuring respiratory air flow and pressure and the simultaneous activity of syringeal and respiratory muscles (see Suthers 1999a, 1999b).

What has been learned from these micro-techniques is enough to make a grown avian bioacoustician giddy, because the two syringes interact in different ways that



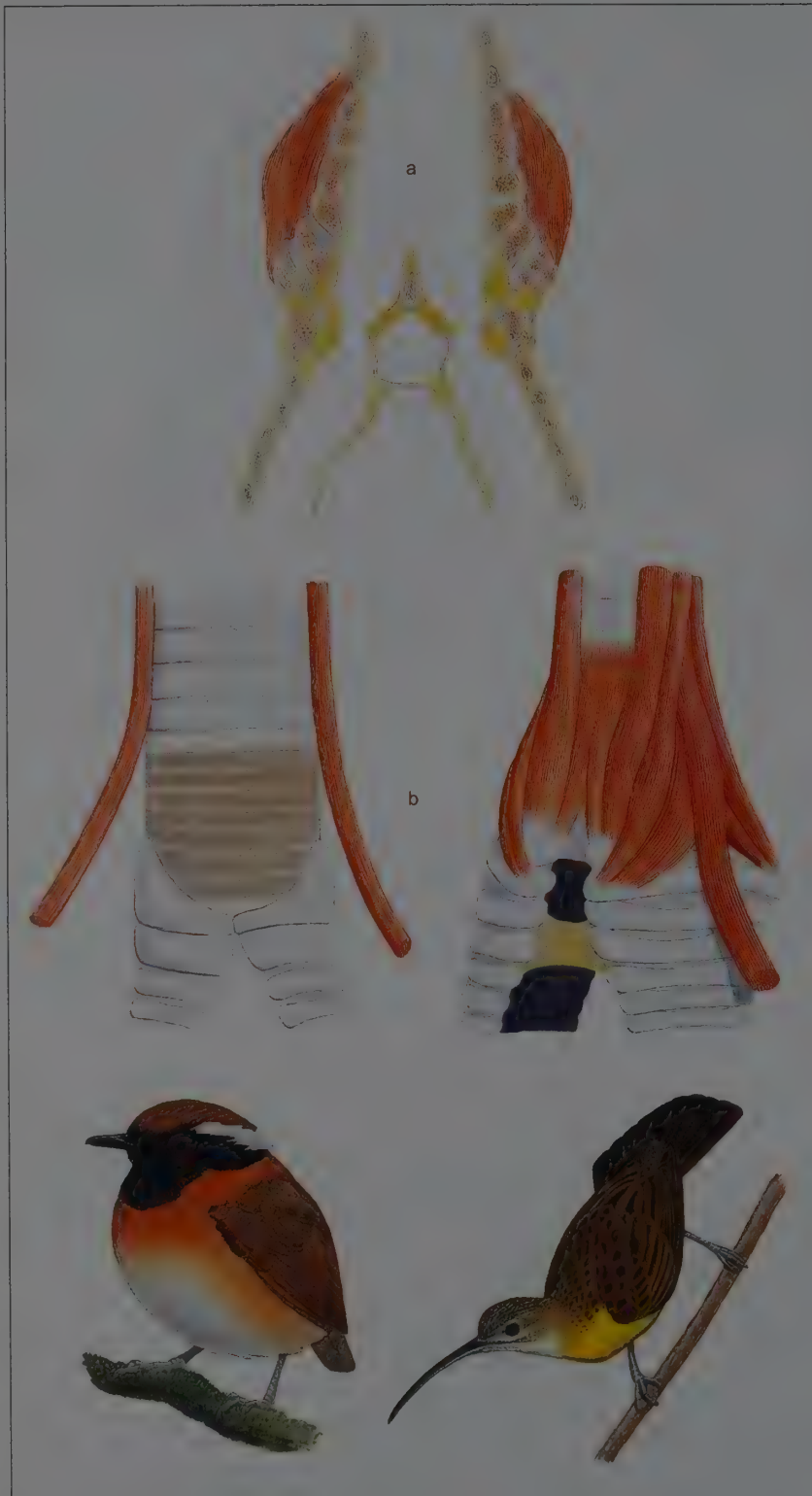


Figure 4. (a) A cross-section of a syrinx, showing major components believed to play a role in producing sounds.

(b) Two passerine syrinxes: a relatively simple one of a suboscine (Chestnut-belted Gnatcatcher *Conopophaga aurita*), showing the single pair of extrinsic muscles, the sternotrachealis; and a more complex syrinx from a songbird (Little Spiderhunter *Arachnothera longirostra*), showing the sternotrachealis and six pairs of internal muscles (after Gill 1995). The songbird's exquisite control of this more complex syrinx is perfected after repeated practice of memorized songs, until the sequence of neural signals and muscle contractions gets it right, so that the bird can routinely produce each song in its repertoire, over and over, with unerring skill.

[Figure by Francesc Jutglar]

allow each species to achieve its own type of vocal virtuosity. In some species, such as the Grey Catbird (*Dumetella carolinensis*) and Brown Thrasher, the left and right syrinx make roughly equal overall contributions to the hundreds (Kroodsma *et al.* 1997) or thousands (Boughey & Thompson 1981) of songs that these birds have mastered (Fig. 5; e.g. Suthers *et al.* 1996). In other species, such as the domesticated Waterslager Canary (*Serinus canaria*), the left syrinx is responsible for about 90% of the song (Suthers & Goller 1998), thus confirming what had been deduced two decades before when the controlling nerve to the left syrinx had been severed (Nottebohm & Nottebohm 1976). Predominant use of only one syrinx may restrict the Waterslager

*In some species, if one side of the syrinx is denervated early enough in life, typical songs can be produced all from one side. How much of syrinx usage is learned?*

Abbot S. Gaunt,  
Ohio State University, Columbus, USA

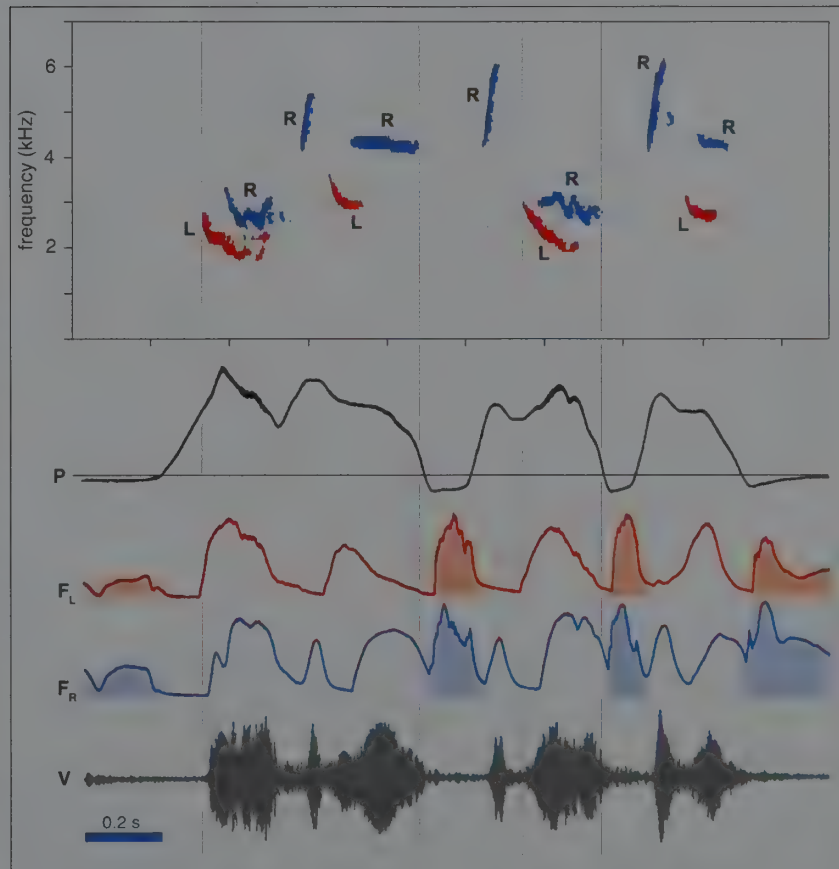
Acoustically complex songs must require great motor skill and precision. Do listeners use these elaborate songs in some species to assess a singer's fitness?

Roderick Suthers,  
Indiana University, Bloomington, USA

Canary to the characteristic low-frequency notes in its song, but other species achieve much broader frequency ranges by using both syrinxes. This point is illustrated well by the songs of the Northern Cardinal (*Cardinalis cardinalis*), which have pure whistled notes sweeping over a broad range of frequencies, from roughly 1 to 7 kHz (Lemon & Chatfield 1971); in each of these sweeping whistles, the two syrinxes are used sequentially, the left syrinx producing sound below about 3.5 to 4.0 kHz and the right syrinx producing sounds above that range (Suthers & Goller 1998). Because of this exquisite coordination of the two syrinxes, the whistle sweeps seamlessly throughout its broad frequency range, with no trace of the separate origins of the upper and lower frequency components. Perhaps most impressive is the song of the Brown-headed Cowbird (*Molothrus ater*), with its abrupt changes in frequency over 1 to 13 kHz (King *et al.* 1980); the frequency contrasts in successive notes are achieved by rapidly alternating use of the left and right syrinx, with the final high whistle note produced by the right syrinx (Allan & Suthers 1994).

Exactly how sounds are produced, however, remains something of a mystery. It was thought, for example, that the sounds in the syrinx were produced by vibration of the membranous walls that extend into the airflow (e.g. Miskimen 1951; Greenewalt 1968). That hypothesis was challenged only recently, when it was shown that destruction of these membranes has little effect on the quality of song produced (Goller &

Figure 5. Secrets of a vocal gymnast revealed, showing how a male Brown Thrasher coordinates the left and right side of his syrinx to produce a few sounds from his enormous repertoire of well over 1000 songs! The sonagram (top) shows the sounds produced, labelled L (left) or R (right) for the side of the syrinx that produced those particular sounds. Evidence of two sound sources operating simultaneously is in the sonagram itself, as the first two sounds produced are not harmonically related (i.e. the upper note is not simply a harmonic of the lower note). The pressure (P) in the air sacs below the two syrinxes is high and positive (above horizontal baseline) when sounds are being produced. The rate of air flow (F) through the left syrinx ( $F_L$ ) and the right syrinx ( $F_R$ ) is correlated perfectly with the timing for sounds revealed in the sonagram (shaded areas indicate mini-inhalations of a fraction of a second, when air pressure P in the air sacs is negative). As labelled in the sonagram, sounds produced by the right syrinx tend to be a higher frequency than those produced by the left syrinx. Note, too, that this sonagram consists of almost two complete renditions of the same series of sounds, and that the gymnast executes the identical moves with the left and right syrinx to produce the two renditions (after Suthers 1999a).



Larsen 1997); instead, it appears that the medial and lateral labia within each syrinx are extended into the airflow, and these labia vibrate as air is forcefully exhaled through the slit between the two labia. The sounds are modulated by the vocal tract (Nowicki 1987), too, and the trachea in some birds is elongated, perhaps by sexual selection in an attempt to exaggerate the size of the vocalizing bird (Fitch 1999). Beak motion also modulates the sounds (Westneat *et al.* 1993), and bill morphology may determine the range of sounds that birds are able to produce, as suggested for Darwin's finches (J. Podos 2000); thus, the food that is eaten may dictate the morphology of the beak, which in turn may restrict the range of possible vocalizations, so that morphology and behavior are inextricably interrelated in sexual selection. Given all that is involved in producing the intricate details of each vocalization (e.g. Lavenex 1999), it is not surprising that Lambrechts & Dhondt (1988) and Lambrechts (1996) proposed that birds physically "tire" from producing one song type repeatedly, and that neuromuscular fatigue has been one reason for the evolution of larger song repertoires (see below).



However these vocalizations are produced, the resulting sounds are the culmination of an extraordinary coordination of syringeal and respiratory muscles (see Vicario 1993) and the vocal tract, a feat that becomes all the more impressive as more is learned about the complexity of bird sounds and how masterfully and precisely they are produced and reproduced. It is no wonder that Donald Borror, a pioneer in North American avian bioacoustics, referred to some of the more remarkable songsters as "vocal gymnasts" (Borror & Reese 1956).

### 3) Signal transmission

Those who listen carefully to birds realize that birds sound different in different environments. In open country, for example, when we are close to a singing bird, songs are often sharp and crisp. In the forest, however, sounds are typically softer, lacking the crisp quality of birds in more open environments. Although the types of sounds that birds make in open and closed habitats may differ somewhat (see below), one of the main reasons we hear them as different is because of the "echoes" (i.e. reverberation) that are caused by dense vegetation. The echo results from sound bouncing off the vegetation, so that the sound reaching our ears directly from the bird's bill is slurred by the sound reaching our ears just a split second later, as it bounces off vegetation. This "blurring" of sound is readily seen in sonagrams, where the onset of a sound is typically sharp but the offset is not, with the notes on the sonagram trailing off in a smear.

Reverberation has implications for how we try to capture bird song on our tape recordings, too. The crisp qualities of a song are best preserved by placing the microphone as close as possible to a singing bird; the greater the distance from which a singing bird is recorded, the more useful is a parabolic microphone, because this highly directional microphone limits the recording of sounds (i.e. echoes) that arrive at the parabola from directions other than the singing bird. Sometimes recordings are so good that they sound unnaturally shrill, but the recordings sound "unnatural" to us only because our ears are highly directional and we are therefore accustomed to hearing sound after it has been degraded by the environment.

The medium between the signaler and receiver is air, of course, and as the signaler and receiver birds become more distant from each other, their sounds are altered by the environment in predictable ways (for an excellent review, see Bradbury & Vehrencamp 1998). Sound is not instantaneous, for example, but travels at 344 m/sec, so that birds at greater distances will experience delays. Sound intensity diminishes with distance from the source, too, this "spreading loss" roughly equal to the square of the distance from the source. Higher frequencies are attenuated more over distance than are lower frequencies. Reverberation varies by habitat, such that rapid amplitude modulations would be obscured in forests (because the echo of one pulse off the trees obscures the next pulse from the bird) but not in open country. Temperature differences between air at and above the ground (e.g. in the canopy) can produce either sound channels, in which sound is trapped and propagated longer distances, or sound shadows, areas in which sound is greatly attenuated. The signaling animal must also contend with background noise, such as from wind, rain, or other animals. Indeed, to be effective, long-distance communication must contend with many environmental factors.

These and other features of sound propagation have implications for the vocalizing bird, which (normally) tries to communicate as effectively and efficiently as possible. Considerable progress is being made in understanding the effects of the environment on signal transmission and the structure of signals themselves. Pioneering these efforts was Morton (1975), who surveyed Neotropical birds and discovered that open-country birds were more likely to use rapid frequency modulations than were forest birds; this result was largely confirmed for North American habitats by Wiley and colleagues (Wiley & Richards 1978, 1982; Wiley 1991). Even within species, songs vary among populations, and it is possible that songs are locally adapted to transmit best through particular habitats (Gish & Morton 1981); the songs that are best adapted to a local habitat might be culturally transmitted by young birds, which would preferentially learn songs the fine details of which were best preserved between the signaler and the receiver (Hansen 1979; Morton *et al.* 1986). The amount of reverberation or degradation in a signal can also be used as an indication of the distance of the vocalizing bird (Richards 1981; Naguib *et al.* 2000), the implications of which remain controversial (Morton *et al.* 1998). Our understanding of the relationship between bird song and habitat structure has been aided by studies of a number of species, such as the Rufous-collared Sparrow (*Zonotrichia capensis*—e.g. Nottebohm 1969; Handford & Loughheed 1991; Loughheed & Handford 1992), the Great Tit (*Parus major*—Hunter & Krebs 1979), the White-throated Sparrow (*Zonotrichia albicollis*—Wasserman 1979; Waas 1988), and paruline warblers (Lemon *et al.* 1981). We also

*How have mechanisms of sound production and learning constrained the diversity of sounds that birds produce, and how do structural limits influence song function?*

Jeffrey Podos,  
University of Massachusetts, Amherst, USA

*How do "noise" and the possibility of "error" affect the evolution of communication, including vocal communication in birds?*

R. Haven Wiley,  
University of North Carolina, Chapel Hill, USA

*What information in a song is lost during long-distance transmission? How do environmental acoustics and other factors influence the evolution of long-range vocal communication?*

Marc Naguib,  
University of Bielefeld, Germany

*Which mechanisms help birds analyze the complex acoustic scenes created by the mixture of different sound sources in their environment?*

Georg M. Klump,  
Technische Universität München, Germany



know that birds vocalize less under suboptimal conditions (e.g. during rain or wind), or avoid masking each other by alternating songs with singers of other species (Ficken *et al.* 1974). All of these evolutionary adjustments in song quality or singing behavior are made in an attempt to maximize the ability of birds to transmit relevant signals in a noisy world (Klump 1996).

#### 4) Signal perception

The complex sound wave that arrives at a bird's ears is converted to nerve impulses by the peripheral auditory system (review in Saunders & Henry 1989). Sound is first concentrated by the external ear (auditory meatus), which is covered by feathers. Sound waves vibrate the tympanic membrane, which transmits these vibrations to the inner ear by a single bone, the columella. Exactly how the fluid-filled cochlea of the inner ear converts these complex vibrations to meaningful nerve signals is unknown, but nerves eventually project the extracted signals to the auditory region in the forebrain, called Field L, which controls how birds hear sounds. How this auditory region interacts with the forebrain's motor regions (i.e. regions that control how birds produce sounds) is an exciting area of inquiry (see next section).

The hearing ability of most birds falls within the range of human hearing (Dooling 1982; Fay 1988). The range of maximum sensitivity for songbirds is roughly 1 to 5 kHz, for example, and non-songbirds, which tend to be larger, hear better at slightly lower frequencies. For some species, hearing acuity may be sharpest in the narrow range where each species produces its sounds (Okanoya & Dooling 1988). Most birds, it seems, do not hear sounds of either very low or very high frequencies outside the range of human hearing.

Despite of having small heads with short distances between the ears, birds are able to determine direction and distance rather well. Rufous-sided Towhees (*Pipilo erythrophthalmus*), for example, determined distance to within 7% accuracy and azimuth within 5 degrees (Nelson & Stoddard 1998). Distance clues are provided in a sound by the amount of reverberation (see above), but birds also use the amplitude of the sound to estimate distance (Phillmore *et al.* 1998; Nelson 2000).

Some species clearly have special hearing abilities. The Rock Pigeon (*Columba livia*) can hear in the 1 to 10 Hz range (Kreithen & Quine 1979), a range that we humans call "infrasound" because it is well below our range of hearing. Oilbirds (*Steatornis caripensis*) and Cave Swiftlets (*Collocalia linchi*) probe the dark with brief (1 to 20 msec), audible clicks of 2 to 15 kHz, using the echoes to navigate (Medway & Pye 1977; Konishi & Knudsen 1979). Common Barn-owls (*Tyto alba*) are renowned for their ability to locate prey in complete darkness (Payne 1971); these special auditory skills are achieved, in part, by an asymmetrical arrangement of the two ears, with the left facing downward and the right facing upward, enabling the owl to pinpoint sound sources in both the horizontal and the vertical plane (Knudson 1981). Thirty to 40 years ago it was thought that birds had special abilities to hear rapidly occurring sounds (i.e. an excellent "temporal resolving power"), perhaps up to 10 times better than we could hear (e.g. see Schwartzkopff 1973). When birds were tested in the laboratory, however, the results were surprising: birds appeared to be no better than us humans (Dooling 1982). New testing procedures now favor the birds again, it seems. Unless they can hear far better than we can, it is certainly a mystery how young birds are able to copy the precise details of songs, whose details which we cannot begin to appreciate with the unaided ear. Clearly, much remains to be learned about how well birds hear and the role of hearing in their lives.

#### 5) Neural control of bird song

Given the impressive abilities of songbirds to learn and produce large repertoires of songs and the apparent importance of those abilities in sexual selection (see below), we should expect complex neural control of these feats, too. During the last 30 years, neurobiologists probing the brains of songbirds have revealed discrete neural pathways for producing and hearing songs (Fig. 6; sample reviews in Konishi 1989; Nottebohm 1989, 1999; Brenowitz & Kroodsma 1996; Brenowitz *et al.* 1997). What has been revealed in this area of research is exciting and is progressing rapidly (Marler & Doupe 2000).

Several studies have now revealed that the number of different songs a bird sings is positively correlated with "brain space", or the volume of certain clusters of neurons (i.e. song nuclei) in the forebrain. This relationship was first discovered in the Common Canary, in which the repertoire of a male's song syllables is correlated with

What would Luis say about parallelism in sound perception between birds and people despite very different brains? Birds can perceive sequences of notes as units; do birds perceive these units as we humans perceive musical melodies?"

Hansruedie Güttinger,  
Universität Kaiserslautern, Germany

What are the inner ear mechanisms that make birds 3-5 times more sensitive than humans to changes in the temporal fine structure of complex sounds (such as bird vocalizations)?

Robert J. Dooling,  
University of Maryland, College Park, USA

How can birds perceive the details of songs well enough to copy them, while we cannot perceive these details at all?

Philip K. Stoddard,  
Florida International University, Miami, USA

the volume of two forebrain nuclei, HVC and RA (Nottebohm *et al.* 1981). Similar relationships have now been found in other species, such as the Marsh Wren (*Cistothorus palustris*—Canady *et al.* 1984), several Neotropical duetting wrens (Brenowitz & Arnold 1986), and, indeed, in a broad comparative analysis of 41 songbird species in 9 different families (DeVoogd *et al.* 1993). Needing more brain tissue with a larger repertoire must be costly, but this increased investment in song-control centers is apparently needed so that a bird can learn and manage its larger song repertoire. Because the volume of the song nuclei in Marsh Wrens does not increase as more songs are learned, it seems that the size of the song nucleus with which a young bird is endowed dictates how many songs he will be able to learn (Brenowitz *et al.* 1995). Exactly how or where songs are stored in the brain is unknown, but the volume of song-control nuclei is apparently influenced by both the number and the size of the neurons in these song-control centers, and the density of dendritic spines does increase in certain nuclei as more songs are learned (Airey *et al.* 2000).

Another intriguing feature of these forebrain song nuclei is their remarkable seasonal plasticity (Nottebohm 1981), as several of them are up to 70% larger in breeding birds than in non-breeding birds (review in Brenowitz & Kroodsma 1996). One exciting aspect of this plasticity is that adult songbirds generate new neurons that migrate to and are incorporated into these song-control centers (e.g. Álvarez-Buylla *et al.* 1990). But why these brain features change with the seasons remains a mystery. Initially it was proposed that the seasonal fluctuations were related to the annual learning of new songs, such as by the Common Canary, but seasonal plasticity also occurs in species that do not learn to sing new songs each year (Brenowitz *et al.* 1991).

So much more remains to be learned about how the brain controls song perception and production in birds (e.g. see Brenowitz & Kroodsma 1996). Just where and how, for example, are the sensory models of songs stored in the brain? What role do all of the song-control centers play during development (Bottjer & Arnold 1997), as the young male first memorizes his songs and then, even while sleeping, practises them (Dave & Margoliash 2000)? The discrete vocal-control nuclei are remarkably similar but are believed to have evolved independently in the brains of songbirds, parrots and hummingbirds, suggesting that the brain is constrained in how it controls these learning tasks (see Jarvis & Mello 2000; Jarvis *et al.* 2000); what other homologies or analogies might be found as vocal learning is discovered in other groups, too? How are the neural and endocrine systems interrelated in their control of song (Ball & Hulse 1998; Ball 1999)? What is the neural basis for how non-singing females learn to recognize different songs, and for singing females what factors regulate the development of this neural control system (Nottebohm & Arnold 1976; Arnold *et al.* 1996)? As species other than the convenient laboratory canary and Zebra Finch (*Taeniopygia guttata*) are studied, what might we learn about how neural and endocrine systems are adapted to different life histories?

## How sounds develop in individuals

From the embryo to an accomplished vocalist (or instrumentalist), a rather remarkable transformation occurs. The sounds used by individuals change over time, but, at all stages of life, the appropriate sounds are available to help manage a social environment, and largely for selfish gain. From the best mimics to the most selective of learners (to those which do not learn at all), each species seems to have its own genetically-endowed blueprint as to how to proceed through this developmental process (e.g. see Mundinger 1999). Understanding how birds acquire their sounds and the ability to use them has received much attention, as we try to understand the role of nature and nurture, the ecological or social circumstances that might favor different kinds of vocal development, and so many other features of how birds acquire the sounds they use to communicate. In this section, we review several of these areas.

### 1) Nature versus nurture

As a young bird matures, it becomes competent in using the vocal repertoire of adults. Exactly how that youngster becomes competent has been a focus of considerable debate (e.g. Johnston 1988), but the broad issues are rather simple, with developmental styles perhaps best viewed along a continuum. At one end of the continuum are sounds that develop normally in an individual regardless of what it experiences as it matures. At the other end of the continuum are sounds that the young bird must imitate from

*How and where are song memories acquired in youth encoded and stored? How and where is auditory feedback information encoded and stored?*

Mark Konishi,  
California Institute of Technology, USA

*Does dreaming about singing help solidify patterns learned during the day? Can this give us insight into how humans learn? And so, did Luis dream of bird songs? I think he must have.*

Daniel Margoliash,  
University of Chicago, USA

*What cellular and molecular mechanisms produce sex differences in the vocal apparatus and neural systems controlling bird vocalizations?*

Arthur P. Arnold,  
University of California, Los Angeles, USA

*Could vocal learning and its associated brain structures have been present in the common ancestor of all tetrapod vertebrates, including reptiles, mammals, birds, and even dinosaurs?*

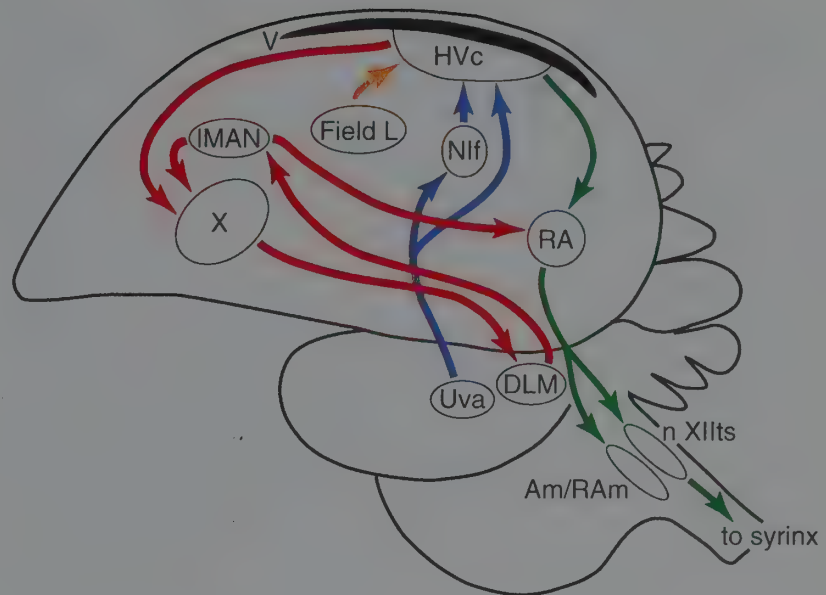
Erich D. Jarvis,  
Duke University Medical Center, Durham,  
North Carolina, USA

*Is the storage and retrieval of song memories similar in female and male songbirds, despite often very different song control systems?*

Gregory F. Ball,  
Johns Hopkins University, Baltimore, USA



Figure 6. The amazing “bird-brain”, revealing an extraordinary network of brain “nuclei” (groups of neurons) that are involved in controlling how birds learn and produce songs. The pathway in red indicates the anterior forebrain pathway that is essential for song-learning. This pathway connects HVc and area X in the telencephalon of the forebrain to a nucleus DLM in the thalamus and the lateral (l) part of the nucleus MAN in the telencephalon. IMAN also projects back to area X, which provides the potential for feedback within this pathway. The second pathway controls the motor production of song and is shown by the blue and green arrows. The blue arrows indicate connections to HVc from the nucleus Uva in the thalamus and Nlf in the telencephalon. The green arrows indicate the connections from HVc to RA, and thence to nucleus nXlts in the brainstem, which controls the muscles of the syrinx. RA is also connected to the brainstem nuclei RAm, which controls the muscles responsible for exhalation, and Am, which regulates muscles of the larynx. Field L is an auditory region in the forebrain that connects to HVc. Figure kindly supplied by Eliot A. Brenowitz.



adults, and, without proper “tutoring” by adults, the sounds that the maturing bird produces are highly abnormal.

Among birds, one can readily find examples at both ends of the continuum and at all points in between (e.g. see Slater 1989). An example of songs that are largely genetically inherited is that of a New World suboscine flycatcher, the Eastern Phoebe (*Sayornis phoebe*—Kroodsma 1985; Kroodsma & Konishi 1991). Each male of this species has two different songs, the *fizz-bew* and the *fitz-bew*, and the young birds, regardless of their auditory experience, develop seemingly normal songs. Songs develop normally even if young birds are deafened so that they cannot hear themselves practise. (Depriving a young bird of this “auditory feedback” during development is the crucial test to determine the extent to which songs are encoded directly in the genes, or, put another way, the extent to which songs must be learned (see following paragraphs).

At the other end of this developmental spectrum are numerous examples of how songbirds must learn the details of their songs from accomplished adults. One of the earliest demonstrations of this phenomenon was by Barrington (1773) over two centuries ago (see above). It is William Thorpe (e.g. 1958, 1961), however, who is considered the pioneer of the scientific study of song-learning in birds. Thorpe demonstrated that young Chaffinches (*Fringilla coelebs*) would imitate songs from loudspeakers, that young birds isolated from adult songs would develop aberrant songs, and that the learning was concentrated in the first year of life. Other biologists soon followed, with Thorpe’s student Peter Marler moving to the New World and beginning his classic studies of song-learning among White-crowned Sparrows (*Zonotrichia leucophrys*—Marler & Tamura 1962, 1964; Marler 1970b). And students of Marler, in turn, would continue the quest for understanding how young songbirds learn their songs (e.g. Konishi 1963, 1965; Nottebohm 1968, 1970). Elsewhere, in Germany Immelmann (1969) began his studies of the Zebra Finch, and Thielcke (1965) his studies of creepers (*Certhia* spp.). Laboratories everywhere were soon exploring these remarkable song-learning abilities of songbirds (e.g. see Kroodsma & Baylis 1982).

What was learned from these early studies suggested a two-step model for song-learning (reviewed in Nottebohm 1999). First the young bird memorizes the required sound and stores it in the brain. Some time later, from days to months depending on the species, the maturing bird begins to practise that sound, learning to match its voice with the stored template in the brain. Initial attempts are unrecognizable warblings (i.e. subsong), but gradually the practice improves (plastic song), until the song produced is a good match of the memory in the brain. Once the songs have reached their stable adult form, they often remain essentially unchanged throughout the life of the individual (e.g. Ewert & Kroodsma 1994). This stability seems to be maintained in some species even without auditory feedback (i.e. when the singer is deafened—Konishi 1965), but in other species the song begins to deteriorate immediately after loss of hearing (Bengalese Finch *Lonchura striata*—Okanoya & Yamaguchi 1997). Thus, the extent to which adult birds are constantly “relearning” their songs as they sing may differ among species.

Does the complexity of an adult bird’s song determine how much auditory feedback is required to maintain that song throughout life?

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The characteristics of songs that need to be learned from adults vary among species. At one extreme are species like the White-crowned Sparrow and Anna's Hummingbird (*Calypte anna*), which must learn frequency, syllable structure, and rhythm of the song (Marler 1970b; Baptista & Petrinovich 1984; Baptista & Schuchmann 1990). In other species, certain characteristics such as the rhythm of the song's components might develop independently of experience (e.g. European Greenfinch *Carduelis chloris*—Güttinger 1979). In European creepers, the song's notes seem to develop normally without experience, because they are derived from the begging calls of the juvenile; to sing the local dialect, however, juveniles must learn the permutations and combinations of the different "inherited" call notes from adults in the population (Thielcke 1970a). The features of the song that must be learned from other adults are minimized for species in which individuals improvise, or make up, their song repertoires. Young Sedge Wrens (*Cistothorus platensis*) and Grey Catbirds can acquire hundreds of different songs in this fashion (Kroodsma, Houlihan *et al.* 1997, Kroodsma, Liu *et al.* 1999); because no fine details of songs are imitated from other individuals, the song repertoires of different individuals are highly distinctive, yet fall within the inherited guidelines dictated by an internal song-generator. In the two-step model of song-learning, these improvisers perhaps do not need the first step, that of memorizing model songs; maybe they still require auditory feedback during song practice, as they learn to match their song output to this internal pattern-generator.

## 2) Ecology of vocal learning in songbirds

Questions about "how much is learned" are quickly followed by a host of other questions, such as "Where, from whom, and when are songs learned?" Consider a juvenile male White-crowned Sparrow in the coastal chaparral of California, for example. His father has a song typical of the local dialect area, which consists of several hundred males all singing the same song pattern (Marler & Tamura 1962; Baptista 1975). As the young male hears his father's song, the species-typical introductory whistle seems to be a cue to learn what follows (Soha & Marler 2000); he memorizes the details of that song, to an extent that he could use that memory later to develop his own song. When this young male disperses from his natal territory to his breeding territory, however, he might encounter a sharp boundary between two different dialect areas. If he chooses to stay and breed within his own dialect area, he can simply perfect the song in his memory (perhaps refining the song to match the details sung by immediate neighbors—Trainer 1983), but if he crosses the boundary to the new dialect area, he must learn a new song in order to fit in there. The implications of his choice are important, because the relationship between song dialects and genetic population structure is at stake, and whether or not song-learning and song dialects tend to isolate neighboring populations and hasten speciation. How to gather good data on this topic and how to interpret them has been hotly debated (see Baker & Cunningham 1985 and accompanying commentaries).

The answers to these questions are far from complete and certainly differ among species, but some answers are in hand. We have learned, for example, that answers to these kinds of questions must be pursued in nature, because how young birds behave in the highly artificial laboratory environments can differ substantially from how they behave under natural conditions (e.g. see Beecher 1996; Baptista 1999; Liu & Kroodsma 1999; Liu 2001). When young marked birds have been followed in nature, they do cross dialect boundaries and settle in neighborhoods with songs that differ from those of their father, whether the species be Bewick's Wrens (*Thryomanes bewickii*—Kroodsma 1974) in Oregon, USA, or Saddlebacks (*Philesturnus carunculatus*—Jenkins 1978) in New Zealand. Young White-crowned Sparrows disperse across dialect boundaries, too (Baker & Mewaldt 1978; Petrinovich *et al.* 1981; DeWolfe *et al.* 1989; Bell *et al.* 1998). After moving to a new song neighborhood, new song memories are acquired, and songs of the new location are practised and eventually produced (O'Loughlen & Rothstein 1995), although traces of the father's songs are sometimes still detectable (Kroodsma 1974; Bell *et al.* 1998).

For some species, song-learning "rules" can be identified. Field studies of the sedentary Song Sparrow in Seattle, Washington, have revealed that a young male during his hatching summer copies entire songs (up to 10) from individual males in a small neighborhood where he will eventually establish his territory; a young male preferentially learns songs that are shared among his neighbors, too, as if to maximize the probability that he will share songs with those neighbors that survive to his first (and subsequent) breeding season (see Beecher 1996; Beecher, Stoddard *et al.* 1996, Beecher, Campbell *et al.* 2000; Nordby *et al.* 1999). Essentially these same rules are followed by the migratory Chipping Sparrow (*Spizella passerina*) in western Massa-

*Do the abnormal songs of songbirds raised in acoustic isolation reflect all the knowledge that a young bird has about the species-typical song pattern?*

Jörg Böhner,  
Technical University of Berlin, Germany

*How does vocal learning affect the dynamics of evolutionary processes in which song plays a role, like sexual selection and speciation?*

Carel ten Cate,  
University of Leiden, Netherlands



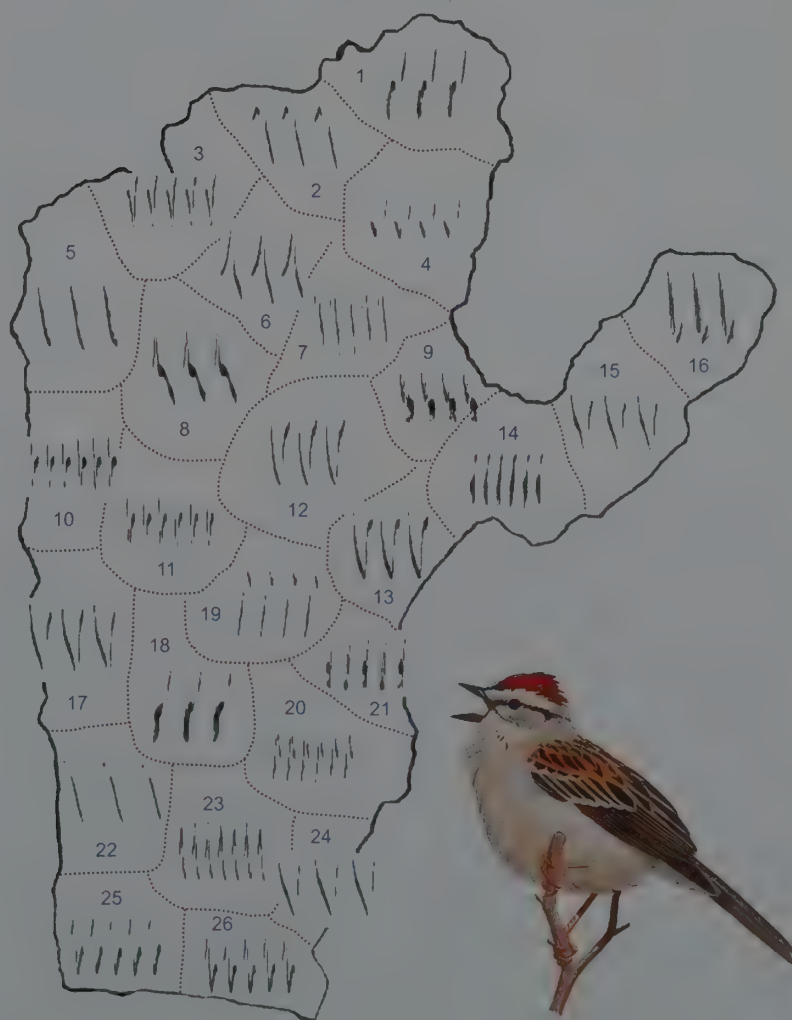
chusetts (Fig. 7). This sparrow also learns his single song at his breeding location, either during his hatching summer (like the Song Sparrow) or after migration the following spring (Liu 2001). Migratory young male Indigo Buntings (*Passerina cyanea*) also learn songs of adult neighbors after their first migration (Payne 1996).

Although learning songs at the breeding location seems to be a general pattern (see also Payne & Payne 1997), there are exceptions. One is found among the Galapagos finches, in which sons sing primarily the songs of their fathers (Millington & Price 1985; Gibbs 1990; Grant & Grant 1996). Another possible example is the Zebra Finch (Slater & Mann 1990; Zann 1997). Why species differ in their song-learning strategies remains largely a mystery, in part because the functions of songs and "song-matching" (an exchange during which males respond to each other with their identical, learned songs) are so poorly understood (see below).

Other aspects of song development must have an ecological basis, too, such as the extent to which males imitate or improvise their songs. For this question, New World wrens in the genus *Cistothorus* provide a glimpse of an answer. North American Marsh Wrens imitate precise details of their large song repertoires and tend to be site-faithful, with males forming stable singing communities in which their imitated songs can be hurled incisively at each other during matched-countersinging duels (review in Kroodsma & Verner 1997). In contrast, North American Sedge Wrens improvise their large repertoires, and populations are not site-faithful, such that a singing male wren cannot expect to interact with the same other wrens for more than a month or so during his life (Kroodsma, Liu *et al.* 1999). When populations of this Sedge Wren are sedentary, however, as in the Neotropics, more song-learning occurs, local dialects exist, and males countersinging with matching song types, suggesting that in these *Cistothorus* wrens site-fidelity promotes song imitation and lack of site-fidelity promotes song improvisation (Kroodsma, Sánchez *et al.* 1999).

Figure 7. Amid the great diversity of song types used by Chipping Sparrows, micro-dialects are created when a young male, after dispersal, rejects whatever he had learned from his father and learns the song of one particular male at his future breeding location.

Illustrated here are partial sonagrams of the songs of 26 males on their 1997 breeding territories at the Quabbin Cemetery in western Massachusetts, USA. Male 16 was the father of male 13, who learned his song from male 12. Male 8 was the father of male 25, who learned his song from male 26. Both male 12 and male 26 were also present in 1996, so the juvenile could have learned his song during either his hatching year or the following spring. These micro-dialects are disrupted when adults disperse to other territories in subsequent years: e.g. males 17 and 24 were neighbors in 1996, the previous year (from Liu 2001).



### 3) And so much more

Many other questions, too, have been the focus of studies of vocal development, especially in laboratory settings. One such question has focused on the timing of vocal learning, and several studies revealed that young birds concentrate their song-learning into a "sensitive period" early in life. A young Chaffinch does not learn new songs after the early spring of its second year (Thorpe 1958), for example, and a young White-crowned Sparrow learns most readily during its first 50 days of life (Marler 1970b). The Marsh Wren's peak of learning sensitivity occurs from roughly day 20 to day 60 (Kroodsmas 1978a). The convenient Zebra Finch has been the focus of a flurry of studies, too (Immelmann 1969; Slater *et al.* 1988), showing that song-learning is concentrated into the first 2 to 3 months of life. In most species, it is as if young birds are "eager" to begin memorizing their songs (even though changes may be made later), as if organizing the neurons and acquiring early memories were crucial for later success. The timing of this early song memorization is relatively impervious to external factors, such as photoperiod, as in White-crowned Sparrows (Whaling *et al.* 1998). In the appropriate social circumstances, however, learning by these species can occur beyond these "most sensitive" periods (Pepperberg 1985).

In other species, new songs are routinely learned throughout life. Male Common Canaries continue to add new components to their song each year (Nottebohm *et al.* 1986), as do Northern Mockingbirds (Derrickson 1987) and the ubiquitous Common Starling (*Sturnus vulgaris*—Eens *et al.* 1992; Eens 1997; Hausberger 1997). Many other species probably learn throughout life, too, but collecting information on this phenomenon in nature is difficult, because a marked bird is not easy to follow and record throughout its life.

Exactly when each species learns its songs is best considered as falling on a continuum that begins early in life and ends at death. Roughly where each species falls on this continuum can be determined in the laboratory, but one should keep in mind several caveats. A species may occupy a broad stretch of the continuum, for example, and not a single point, because strategies of individuals even within a population may differ; a nestling male hatching early in a breeding season might complete its learning during its hatching summer, whereas a male raised late in a breeding season and hearing no songs during his hatching summer will be more likely to defer learning until the following spring (Kroodsmas & Pickert 1980). Where a species falls on this continuum can also be influenced by (sometimes unknown) factors in our highly artificial laboratory conditions, even by the color of the leg-bands on the particular Zebra Finches used in an experiment (Pearson *et al.* 1999) or by a variety of other, sometimes subtle conditions (Slater *et al.* 1988).

One highly artificial condition in the laboratory, of course, is the social environment in which the young bird is learning its song (Pepperberg 1985). A loudspeaker is a highly unnatural tutor, and several studies have shown that young birds are more responsive to live tutors than to loudspeakers (Baptista & Petrinovich 1984; Kroodsmas & Pickert 1984). For some paruline warblers, which use different songs in different contexts (e.g. Staicer 1996a), strategies for developing the two songs differ (Lemon *et al.* 1994); in Chestnut-sided Warblers (*Dendroica pensylvanica*), males apparently need a social tutor more for songs used in intense male-male interactions than they do for songs used in solo singing to attract females (Byers & Kroodsmas 1992). The overall literature seems to confirm this enhanced effect of social tutors (Baptista & Gaunt 1997b; but see Nelson 1997; Payne & Payne 1997).

Another fascinating feature of song development is its selectivity, or lack of it. Renowned mimics occur throughout the world (Baylis 1982): the Neotropical Lawrence's Thrush (*Turdus lawrencii*—Hardy & Parker 1997), the Nearctic Northern Mockingbird (Borror 1964), the Australian lyrebirds (and other species—Chisholm 1946; Robinson 1974, 1975), the Common Starling (e.g. West *et al.* 1983; West & King 1990), and African species, too (Harcus 1977a). Mimicry by the Marsh Warbler (*Acrocephalus palustris*) is especially fascinating, because the birds mimic songs from both their European breeding sites and their African overwintering sites (Dowsett-Lemaire 1979). Some interspecific vocal learning is far more focused, with close relatives or potential competitors learning each others' songs, a number of examples occurring throughout Europe (Helb *et al.* 1985) and elsewhere (e.g. the Great Plains of North America—Baker & Boylan 1999). When these species learn each others' songs, they often defend territories against each other and sometimes attract females of the opposite species, too; how these cases of interspecific song-learning will play out over evolutionary time must await future studies.

In contrast, young males of other species select only a narrow range of species-typical songs (e.g. the White-crowned Sparrow—Marler 1970b; Nelson & Marler 1993). This natural preference for learning conspecific song (Konishi 1985) can some-

*Is the traditional distinction between age-limited and open-ended learning real, and if so, what are the selective factors favoring each adaptation?*

Eliot Brenowitz,  
University of Washington, Seattle, USA

*As Luis showed, birds are much more apt to learn songs from live birds than from tape recorders. Precisely what features of social interaction make a live tutor so much more effective than a tape tutor?*

Michael D. Beecher,  
University of Washington, USA

*Why do some birds mimic various sounds? How do these mimics recognize their own species, and do the mimics recognize the species that they mimic?*

Teruyo Oba,  
Natural History Museum and Institute, Chiba, Japan

*In some sibling species of songbirds, males sing to defend interspecific territories, but females choose males of only their own species. Do males and females view these songs differently?*

Jürgen Nicolai,  
Institut für Vogelforschung, Wilhelmshaven,  
and University of Hamburg, Germany



times be overridden, however; when social tutors are provided, young male White-crowned Sparrows then can learn Song Sparrow songs (Baptista & Petrinovich 1986; see also Pepperberg 1997). White-crowned Sparrows can also be tricked to learn songs of other species if the alien song is preceded by the species-typical White-crown whistle, which apparently serves as a cue for song-learning (Soha & Marler 2000).

A special case of interspecific song-learning occurs among the viduine finches (*Vidua* spp.) of Africa (Nicolai 1964; Payne 1973; Payne *et al.* 1998). These finches are brood parasites, and each viduine depends on a specific host waxbill species (Estrildidae) to rear its young. Male viduines learn the songs of their waxbill hosts and use those songs during courtship. In areas where several sibling species of viduines occur sympatrically, the mimicked song of the host is an important cue for females to identify males of their own species.

Another intriguing feature of vocal learning is the “overproduction” that occurs as young birds practise their songs. During the first step of vocal learning, when birds memorize songs, more songs are committed to memory than will eventually be used. These extra songs are practised by the young bird, but he eventually discards them as he hones the final song(s) he chooses to sing (Marler & Peters 1982; Marler 1997). How the young male chooses which songs to discard and which to keep is probably influenced by what other males, especially adults, are singing adjacent to his breeding territory (Nelson & Marler 1994; Beecher *et al.* 1997; Nelson 1999).

Other fascinating examples of vocal learning occur, too. Among cardueline finches, for example, the male and female of a pair may learn each other’s call notes, such that they are distinctive and easily identified in a flock (Mundinger 1970). A tanager, the Thick-billed Euphonia (*Euphonia lanirostris*), mimics the calls of other passerines, and apparently uses those calls to rally those birds to help mob predators (Morton 1976; Remsen 1976). In the Brown-headed Cowbird, the female seems to play some role in directing what songs the male will learn to sing (West & King 1988).

The above overviews, unfortunately, gloss over all of the astonishing details of how young males of particular species learn their songs, so we end this section by highlighting some of those details in relation to how Common Nightingales learn their large repertoires (Fig. 8; review in Todt & Hultsch 1996). Beginning with the PhD thesis of Henrike Hultsch (1980), Hultsch and Todt have revealed how a male learns the precise details of up to 200 different songs from singing males around him. In the laboratory, it can be shown that learning begins at about day 15, with a peak of learning sensitivity during the first three months, during which time the youngster needs to hear songs from a live social tutor (even a human being with a speaker around the neck will suffice, if that person fed the babies since about 6 days of age). Interestingly, the social factor appears less important later in life, when the birds can still learn from loudspeakers alone and do so. And these birds are rapid learners: 10 different song types can be learned in only 10–20 exposures, and 60 different types if heard only once a day for 20 days. Relatively short sequences of several songs are learned intact from different tutors, and the birds themselves will segment longer tutor sequences into “packages” of 3 to 5 song types that almost always occur together during a singing performance. The remarkable abilities of these skilled songsters and the means by which these songs are learned have been honed over evolutionary time, but for what purpose? Issues of function we turn to in the next section.

How are hundreds of sound patterns stored in the memory of large-repertoire singers, and how do their brains manage pattern choice during retrieval?

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Figure 8. The Common Nightingale, an extraordinary songster with a repertoire of up to 200 songs, all of them learned with remarkable skill from adult males (see Todt & Hultsch 1996).

[Photo by Chris Gomersall/  
Bruce Coleman]





## The function of sounds

Birds use different vocal or instrumental sounds in their repertoire to influence each other, i.e. to communicate with each other. The nature of this influence has been the focus of much discussion, such as whether the communication is honest or dishonest, whether animals manage or manipulate each other, and whether the communication is “true” or whether the recipient was unintended (recent review in Bradbury & Vehrencamp 1998). So much information is broadcast that entire networks of listeners can take advantage of each vocalization. These considerations must permeate any discussion of function, and they will recur (though not be stressed) throughout the thoughts presented in this section.

Consider first our use of the words “song” and “call”, words that so far in this foreword have been used rather casually, as if they are two discrete categories (Spector 1992). What has happened over evolutionary time is that many species have one particular sound that has come to be used in a similar context across taxa. These sounds are typically loud, complex, prolonged, and/or delivered from high perches, almost always by the male (temperate regions) but sometimes by the female, too (especially in tropical regions), *as if* the sounds were being used to impress others or to advertise one’s presence. This evolutionary trend is epitomized by the “songbirds”, the highly successful (almost half of all bird species!) suborder of the order Passeriformes in which vocal learning has enabled extreme elaboration of these “songs”. Almost by default, the other (non-song) vocalizations of birds become “calls”.

This quasi-functional distinction between songs and calls is useful, although messy. Some songbirds, for example, seem to use no sound that we would identify as a song (e.g. the Cedar Waxwing *Bombycilla cedrorum*—Witmer *et al.* 1997), and the gargle call of the Black-capped Chickadee (*Parus atricapillus*) is far more complex than is its simple whistled song, the *fee-bee-ee* (Ficken 1981). Why a cross-species classification of songs and calls cannot be rigid is perhaps best illustrated by crows (e.g. American Crow *Corvus brachyrhynchos*—Brown & Farabaugh 1997). When in close contact with other crows within a group, both males and females “sing” a diverse array of clicks, rattles, caws and coos; for long-distance defense of territory, however, the crows use their loud caws, which we think of as “calls”. Crows thus seem to have reversed what we think of as the usual function of songs and calls. Other taxa, such as the 1000 or so suboscines, remind us that songs need not be especially elaborate or complex, either, as most of these species appear not to learn their vocalizations; they get along just fine with a diverse repertoire of simpler vocalizations, with the distinction between “calls” and “songs” unclear in many species. These few examples illustrate that we should use the terms “song” and “call” cautiously, and beware how our initial labelling might influence how we study the functions of various sounds that birds use.

### 1) The function(s) of calls

Using calls to influence others begins early in life. About 48 hours prior to hatching, embryos of Japanese Quail (*Coturnix japonica*) and Northern Bobwhite (*Colinus virginianus*) produce clicking sounds. Embryos that can hear each other hatch more synchronously than do embryos separated two days before the expected hatching time (Vince 1969). Embryonic chicks communicate with parents, too. Budgerigars (*Melopsittacus undulatus*) begin to vocalize about two days before hatching, and playback of these recorded chick sounds into a nestbox stimulates intense incubating behavior by the parents (Berlin & Clark 1998). Young grebes in the egg call as they become cool, undoubtedly stimulating parents to incubate (Brua *et al.* 1996).

Once hatched, nestlings of all species call to communicate their relative hunger to adults; parents monitor these calls and increase feeding rates accordingly (as demonstrated by experimental playbacks with Red-winged Blackbirds *Agelaius phoeniceus* and Yellow-headed Blackbirds *Xanthocephalus xanthocephalus*—Burger & Trout 1979; Price 1998). Parents are so attuned to serving their young that unsuspecting parents can be exploited by the exaggerated vocal displays of the nestlings of brood parasites, such as the Common Cuckoo (*Cuculus canorus*, Kilner *et al.* 1999). The begging calls of the cuckoo are not learned, but simply exaggerated to exploit the predispositions of their foster parents. In contrast, a young cockatoo raised in the nest of another cockatoo species exploits its foster parents by learning the begging calls of its foster siblings, though the young cockatoo’s alarm calls seem more resistant to learning (Rowley & Chapman 1986). In most species, the differences between signals for food and for alarm seem to be known instinctively by young birds (e.g. Buitron & Nuechterlein 1993).

*What kinds of information can birds really extract from acoustic signals under natural conditions?*

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Museo Argentino de Ciencias Naturales,  
Buenos Aires, Argentina

*In nature, long-range communication encompasses several signalers and receivers. To what extent are avian displays and perceptual abilities adaptations to such communication-network environments?*

Peter K. McGregor,  
University of Copenhagen, Denmark

*Compared with oscines, non-passerines are poorly known. Do the vocalizations of these two groups have similar functions and experience similar selective forces?*

Vincent Bretagnolle,  
Centre National de la Recherche Scientifique,  
Beauvoir sur Niort, France

*What are the functions of different vocalizations of permanently paired suboscines, and how are they used or modified in the infrequent event of attracting a mate?*

Mort and Phyllis Isler,  
National Museum of Natural History,  
Washington D.C., USA

*Songbirds produce a variety of sounds besides song. What role do these calls play in social interactions, particularly between mates, relatives, or members of social groups?*

J. Jordan Price,  
University of Minnesota, USA

These calls can be the social glue on which avian societies are based. Through these calls, parents and their offspring of certain species can identify each other, as revealed, for example, in a nice series of experiments on swallows (Hirundinidae—Stoddard & Beecher 1983; Beecher 1990). Within flocks, Black-capped Chickadees reveal flock membership by converging on the same “chick-a-dee” calls (Nowicki 1989; Hughes *et al.* 1998), the four notes of which are combined in various ways to produce an enormous number of different call-types with great potential for conveying information (Hailman *et al.* 1985, 1987). Patriline is identifiable in Stripe-backed Wrens (*Campylorhynchus nuchalis*), because young males learn their call repertoires from older male relatives; the birds can thus easily recognize others within their own family unit, but they can also recognize calls of relatives which have dispersed to other groups (Price 1999). Dialects occur in calls, too, such as in the “gargle” of chickadees (Miyasato & Baker 1999; Baker *et al.* 2000), the “rain call” of Chaffinches (Baptista 1990), and the flight whistle of the Brown-headed Cowbird (Dufty & Hanson 1999). For the cowbird, a male’s flight whistle might be an honest indicator of a male’s age and therefore a good cue for a fertile female (Rothstein & Fleischer 1987), but the dialectal influence of most calls on bird societies is largely unknown.

As adults, birds tend to use their repertoires of relatively simple calls in specific contexts. A Jungle Fowl (*Gallus gallus*), for example, has about nine different sounds in its repertoire (Collias 1987), and uses a long drawn-out “baaaaawk” when a hawk flies overhead, but a “Baak-buk-buk-buk, etc.” when it sights a ground predator, such as a raccoon. Other chickens respond appropriately, looking around and skyward after hearing the “aerial-predator alarm” and around but not up for the “ground-predator alarm”, thus illustrating the functions of these particular calls (Evans & Marler 1991; Marler & Evans 1996).

Aerial and ground predators are identified with different calls by songbirds, too (Marler 1955). Alarms for ground predators are pulsed and easily locatable (“chinks”), but aerial alarm calls tend to be whistles of high frequency, delivered on a sustained pitch that fades in and fades out and is therefore ventriloquial in quality (“seeets”). The difference in locatability of these two sounds was confirmed by testing two captive aerial predators, a Red-tailed Hawk (*Buteo jamaicensis*) and a Great Horned Owl (*Bubo virginianus*), for the ability to locate these two calls of the American Robin (*Turdus migratorius*). Response to playback was recorded by video cameras, revealing that mean orientation error was greater to chinks than to seeets (51.5 degrees versus 124.5 degrees—Brown 1982).

Use of these predator “alarms” might not always be honest, however. Among Neotropical birds, as in Peru, foraging flocks often consist of five to ten species in the same home range throughout the year. In one flock system, the White-winged Shrike-tanager (*Lanio versicolor*) is a “sentinel”, giving alarm calls when danger threatens, and other species rely on the tanager’s vigilance. On some occasions, however, the tanager appears to give false alarms: when the tanager and another individual converge on the same insect, an alarm call by the tanager causes the competitor to hesitate long enough for the tanager to rush in and capture the insect (Munn 1986). Whether or how often individuals might deceive each other for selfish gain is a fascinating area of study.

Another specialized call used by a number of songbirds is the “nest-departure call”, which is given by a female as she leaves the nest. Sample species include the Red-winged Blackbird (Yasukawa 1989; Yasukawa & Searcy 1995) and White-crowned Sparrow (Hill & Lein 1985). An explanation of the exact function of this call remains elusive, but one hypothesis is that it signals the male to be especially alert for predators as his mate is foraging away from the nest.

In general, what we know about the functions of calls in most species is based largely on educated guesswork, although flexible playbacks that enable the investigator to interact with birds are likely to enable great strides in the future (e.g. see Nielsen & Vehrencamp 1995; Dabelsteen & McGregor 1996; Smith & Smith 1996). Years of watching Winter Wrens (*Troglodytes troglodytes*), for example, led Armstrong (1955) to conclude that they use about 14 different calls. Most are given by both sexes, in predictable situations, but Armstrong admitted that the repertoire of different calls is probably more extensive, and that the many calls he classified undoubtedly intergraded with each other and even with song. As with most species, no sonographic analyses are available for the call repertoire of this wren, in part because the function of the more complex songs has been so much more attractive to study (see next section).

## 2) The function(s) of song

So much information is contained in a song. Information about the species is the most obvious (Bremond 1976; Becker 1982), as all species have songs recognizably different



from those of other species (Nelson 1989). One reason species sing differently, of course, is that we base our classifications, at least in part, on song, so that groups with different songs are classified as different species. Beyond this circular aspect of species differences, however, we must beware of a hidden assumption in our thinking: the fact that we humans use song to identify different species does not necessarily mean that songs are different *so that* individuals of a species can recognize each other and prevent hybridization. It is entirely possible that species are distinct only because of intraspecific forces of sexual selection, and that song features of a species exist irrespective of the song features of other species. This possibility seems rather plausible, given the absence of any good examples of character displacement at species boundaries.

Beyond identifying the species, song also routinely identifies the population from which the bird came (DeWolfe & Baptista 1995), as well as the sex (Farabaugh 1982) and individual (Falls 1982; Stoddard 1996). The singer's motivation, too, can be conveyed by patterns of delivery (Kramer *et al.* 1985; Highsmith 1989; Smith 1991), and perhaps age (Nottebohm & Nottebohm 1978), status or overall health (Nowicki, Peters & Podos 1998) by the repertoire size. Selection pressures on song must clash, because, for example, being distinctive as an individual conflicts with adhering to a stereotyped signal for identifying the species (e.g. Nelson 1989).

Presumably all of this information is used to accomplish what has been widely assumed to be the two main functions of songs, "to repel rival males from their territory and to attract and stimulate females to breed with the male" (Catchpole 1989, p. 1046). We consider evidence for each in turn (see also Kroodsma & Byers 1991), then conclude this section with a brief discussion of female song.

**Repelling rivals, i.e. Territoriality.** Indirect evidence that song is used to interact with and repel rival males is abundant. Males often countersing with each other, and a taped song played to a territory-owner will elicit approach, aggressive displays (e.g. wing-quivering, aggressive trilling) and song, revealing that the owner treats the recorded song as if it were from an intruding competitor. Response to this form of playback is greatest at the center of the territory and least at the edge (Ickes & Ficken 1970; Melemis & Falls 1982).

Experimental evidence of a territorial function for male song has been provided by muting the territory-owner. Early experiments provided suggestive evidence for Red-winged Blackbirds (Smith 1979) and Brown-headed Cowbirds (Dufty 1986), but these muted males could neither sing nor call, so the inter-male function of all vocalizations, not just song, was addressed in those experiments. Better evidence for a territorial function of song alone was provided by McDonald (1989), whose muted Seaside Sparrows (*Ammodramus maritima*) could call but not sing. The songless sparrows were delayed in acquiring territories and hampered in maintaining them.

Also providing evidence for a territorial function of song are "speaker-replacement experiments", in which males are removed from their territory and replaced with loud-speakers broadcasting their songs. Beginning with work on Thrush Nightingales (*Luscinia luscinia*) by Goransson *et al.* (1974), a series of studies has demonstrated that song alone can initially deter males from settling on a vacant territory (Krebs 1977; Falls 1988; Searcy 1988; Nowicki, Searcy & Hughes 1998). Deterrence is short-lived, however, as potential settlers eventually encroach on and claim the vacant territory.

Nevertheless, there must be more to the function of song than mere defense of territory. Perhaps the most obvious reason is that, during the non-breeding season, both males and females of some species can use simple call notes to defend territories (Holmes *et al.* 1989), thus showing that song is not the only sound that can be used for territorial defense. This simple observation suggests that song is a special vocalization used by males (and females) to assess one another during crucial mating choices (see next section).

**Song and female choice.** Much of the recent interest in bird song has been related to sexual selection, i.e. to how song might be used by females to assess and choose sexual partners (see early review in Marler 1960; more recent review in Searcy & Yasukawa 1996). Although songs can be used in quiet "negotiations", we more often think of sexual selection and males displaying, perhaps at full aerobic capacity, in an attempt to influence a mating partner. In this section, we review evidence that females are attracted to or stimulated by these loud male songs, beginning with indirect evidence and ending with more direct evidence.

Indirect evidence that song is used to attract females to a territory is also abundant. Bachelor males typically sing much more than do mated males, for example, and naturally or experimentally widowed males sing more than do paired individuals (e.g. Wasserman 1977). In some species, such as the European Sedge Warbler (*Acrocephalus*

*Why do species have different songs?*

Lucia Liu Severinghaus,  
Academia Sinica, Taipei, Taiwan

*Songs vary among individuals and populations of a species. Why do members of the same species sing differently?*

Helene M. Lampe,  
University of Oslo, Norway

*How can birds use singing to negotiate without necessarily having to approach each other for face-to-face interactions?*

W. John Smith,  
University of Pennsylvania, Philadelphia, USA

*Study of acoustic communication in birds has focused disproportionately on the song of one clade of oscines. What will we learn from a broader phylogenetic, geographic and acoustic focus?*

Robert D. Magrath,  
Australian National University,  
Canberra, Australia

*What is it about a bird's song that matters to its listener? Who is listening, to obtain what benefits, and what do songs convey about the singer?*

Steve Nowicki,  
Duke University, Durham, North Carolina, USA

*Do aspects of song or singing behavior reliably signal aggressive intent? And if so, what mechanisms ensure reliability?*

William A. Searcy,  
University of Miami, Florida, USA

*Why do some species of songbirds, but not others, make extensive use of quiet singing in both agonistic and sexual contexts?*

Torben Dabelsteen,  
University of Copenhagen, Denmark

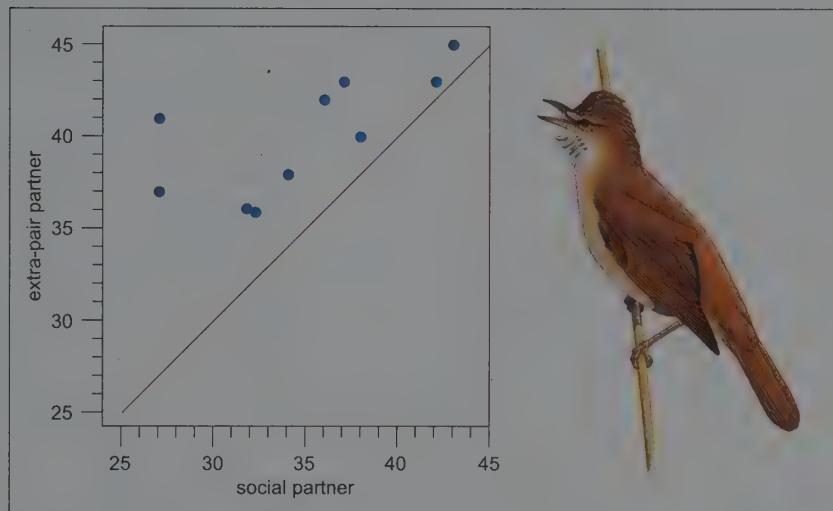


*schoenobaenus*) and California Towhee (*Pipilo crissalis*), males cease singing altogether once paired (Marshall 1964; Catchpole 1973), demonstrating that song probably serves to attract females.

Many studies have also found correlations between male singing behaviors and reproductive success (summary in Searcy & Yasukawa 1996). A male's repertoire size is correlated with his harem size in the Red-winged Blackbird (Yasukawa *et al.* 1980), for example, as it is in the Great Reed Warbler (*Acrocephalus arundinaceus*—Catchpole 1986). Among certain species of paruline warblers, males which successfully attracted a female used a greater diversity of songs than did unpaired males (Spector 1992). An exciting recent correlation was found by Hasselquist *et al.* (1996), who showed that song repertoire size in the Great Reed Warbler was correlated with the male's suitability as an extra-pair partner and with the survival of his offspring (Fig. 9).

Figure 9. If a female Great Reed Warbler is to have an extra-pair partner, she chooses a male which has a larger song repertoire size than does her social partner, with whom she raises her offspring. Here, all 10 females with extra-pair young in their nests obtained their extra-pair young by mating with a neighboring male which had a larger song repertoire than her social partner, as shown by all 10 data points lying above the line of equal repertoire size for the two categories of potential mates. Whether these 10 females used the repertoire size as a cue or some other factor correlated with repertoire size is unknown (data from Hasselquist *et al.* 1996).

Social	Extra-pair
34	38
38	40
32	36
36	42
32	36
42	43
43	45
27	41
37	43
27	37



There is danger in accepting correlations as showing cause and effect, however, as demonstrated by a closer look at the above four examples. For the first two studies, male repertoire size was found to be highly correlated with age or territory quality, such that the statistical effects of repertoire size on harem size were no longer significant. For the warblers, at any given time the vocal behavior of a male is correlated with his mating status, but pairing causes a larger repertoire to be used, not vice versa. Only in the study by Hasselquist *et al.* (1996) are there no known confounding explanations.

More direct evidence of the effects of song on females can be obtained from testing female responses to male song (Searcy 1992). One widely used technique is to play different song stimuli to females and measure the number or intensity of the copulation-solicitation displays that the vocalization elicits (King & West 1977). This technique has been used frequently to address two particular questions: whether a female responds differently to songs of her own and those of a foreign dialect, and whether the female responds more to a larger song repertoire (see additional discussion below). Although the quality of these playback experiments continues to suffer from lack of adequate replication of the playback stimuli (McGregor *et al.* 1992; Kroodsma *et al.* 2001), most studies reveal that females are attentive to the details of song stimuli: they respond more to songs of their own dialects and to "more variable" singing (though not necessarily larger song repertoires, because most experimental designs cannot distinguish between different levels of variability in the songs—Kroodsma 1990). Playbacks can also be used in the field; Logan (1983) observed, for example, that male Northern Mockingbirds sing intensely as females begin a new nesting cycle, and females renested earlier if they heard playback of male song (Logan *et al.* 1990).

Several studies suggest that male quality, or the quality of his territory, might be honestly encoded in how he sings. In Willow Warblers (*Phylloscopus trochilus*), the quality of a territory seems to determine the rate at which a male is able to sing, and males which sing faster attract females earlier (Radesater *et al.* 1987; Radesater & Jakobsson 1989). Female Barn Swallows (*Hirundo rustica*) also seem to prefer males which sing at faster rates (Moller *et al.* 1998), and faster rates may directly reflect male health (Saino *et al.* 1997). In the Neotropics, the rate of singing also seems important for a lekking Ochre-bellied Flycatcher (*Mionectes oleagineus*), as his song rate is correlated with how many females (and other males) visit him (Westcott 1992).

What information does a male mockingbird's song provide to his mate that entices the female to renest?

Cheryl A. Logan,  
University of North Carolina at Greensboro, USA

In another Neotropical lekking species, the Long-tailed Manakin (*Chiroxiphia linearis*), how well two cooperating males match the frequency of each other's song predicts how many females will visit them (Trainer & McDonald 1995). Male health might also be encoded in the duration of songs during the dawn chorus, because song duration can predict the source of extra-pair offspring in Blue Tits (*Parus caeruleus*—Kempnaers *et al.* 1997). The act of singing itself might not be energetically expensive (see Horn *et al.* 1995; Eberhardt 1996; Gaunt *et al.* 1996), but honesty may well be a feature of many aspects of male song (and other vocalizations), thus enabling females readily to compare males (Gibson & Bradbury 1985; Rothstein & Fleischer 1987; Staicer 1996b).

The most convincing evidence of an influence of male song on females comes from experiments in which male song is manipulated and mating success is changed accordingly. One approach is to increase the amount of singing by free-living males by providing extra food; such an experiment with Pied Flycatchers (*Ficedula hypoleuca*) showed that food-supplemented males sang at higher rates and attracted females earlier than did control males (Alatalo *et al.* 1990). Similar approaches, in which only features of song (and not other features, such as the quality of the territory in the Pied Flycatcher example) are manipulated, are needed to test effects of song on females. One possibility is that different vocal behaviors could be "assigned" at random to different males in a laboratory setting. Repertoire size can be manipulated in Marsh Wrens from eastern North America, for example, with males learning as few as 5 or as many as 45 different songs (Brenowitz *et al.* 1995); if a sufficiently naturalistic laboratory setting could be established, the differential attractiveness of these males to females would be the most conclusive kind of test for an effect of repertoire size on mating preferences (Kroodtsma & Byers 1991). This type of manipulative test, in which behaviors are assigned at random to different males, would provide the strongest test for how a particular male vocal behavior influences female choice.

Exactly how male song can influence females is revealed by a number of experiments. Song can stimulate hormonal activity, for example (Brockway 1965; Tchernichovski *et al.* 1998). In African Collared-doves (*Streptopelia roseogrisea*) male songs stimulate females to vocalize and the female's own vocalizations stimulate oogenesis (Cheng 1992). In White-crowned Sparrows, song acts synergistically with photoperiod in stimulating gonadal growth (Morton *et al.* 1985): females exposed to taped male song and long photoperiods (e.g. LD14:10) had faster rates of gonadal growth than did females exposed to long photoperiods but deprived of song. In canaries (Leboucher *et al.* 1998), song stimulates nest-building activities, and even naive, inexperienced yearling females that hear songs have shorter egg-laying latencies and lay larger clutches than do yearlings which do not hear song. Songs with particular phrases ("sexy" phrases) are especially likely to elicit copulation-solicitation displays from females. These experiments with canaries demonstrate not only the overall effects of song quality but also the effects of particular song components on stimulating various reproductive activities in female canaries (Kreutzer *et al.* 1992, 1996).

Perhaps one of the greatest unexplored phenomena that should help us understand how song is used to influence females (and other males) is the dawn chorus (Mace 1987; Staicer *et al.* 1996). During the 30-60 minutes just before sunrise, the intensity of singing, at least in temperate zones, is extraordinary. Males sing rapidly, frequently switching song types (indicating high motivation—see below), sometimes filling the void between songs with call notes (e.g. Spector 1991), as if the intensity of the behavior dictated success. Sometimes singing males of otherwise territorial species gather at dawn in lek-like arenas, as do Chipping Sparrows, with up to 4 birds from neighboring territories singing in intense face-offs on the ground within a few metres of each other (Fig. 10; Liu 2001). The singing interactions among males at dawn may be monitored by females, whose (extra-pair) mating decisions might be based on who wins or loses the dawn vocal duels (Otter, Chruszcz & Ratcliffe 1997; Otter, McGregor *et al.* 1999). If extra-pair mating opportunities are reduced, the dawn chorus might be reduced, too, as in synchronously nesting tropical species (Morton 1996a). There certainly seems to be no better time of day than dawn, after males have fasted all night, for females to demand a performance on which they will base their decisions. The dawn chorus undoubtedly has much to reveal about the functions of song.

**Female song.** The study of singing in females has been a long-neglected field (Ratcliffe & Otter 1996), as reflected by the focus of our review. This neglect is probably due largely to the geographic locations where most bioacousticians study birds, in the temperate zone. If we lived in the tropics, our emphases would be different, as that is where females of many species do sing, such as wrens (Levin 1996), waxbills (Estrildinae—Güttinger 1976), grassquits (*Tiaris*—Baptista 1978), and many others (e.g. Farabaugh 1982).

*Birds often sing many times daily. Costs may include predation risk and reduced time for other activities, but what are the energetic costs of song?*

Millicent S. Ficken,  
University of Wisconsin, Milwaukee, USA

*Do some parts of a male's song require great ability to sing, and, if so, do other individuals listen especially to those parts to identify a healthy male?*

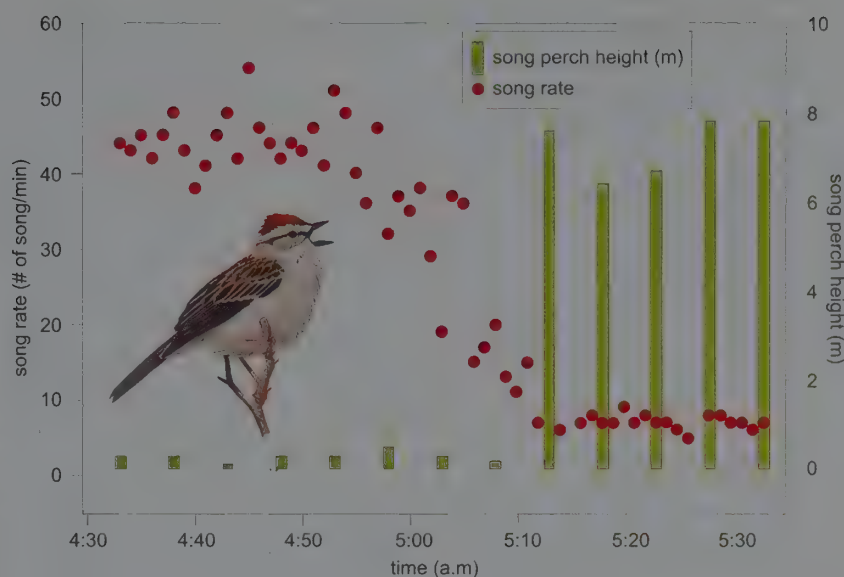
Michel Kreutzer, Université de Paris, France

*How has the importance of extra-pair fertilization in mating systems influenced the function of song and latitudinal differences in its use?*

Eugene S. Morton,  
Smithsonian Institution, Washington D.C., USA



Figure 10. The singing frenzy during the dawn chorus, as illustrated by song rate and perch height in Chipping Sparrows. Before sunrise (about 5:10 A.M.), male sparrows sing short songs at high rates while displaying in lek-like arenas on the ground at their territory boundaries. After sunrise, songs assume their standard daytime length and males then sing more leisurely from the tops of trees nearer the center of their territories (from Liu 2001).



Why is female song so rare among oscine passerines that do not duet?

Jon C. Barlow,  
Royal Ontario Museum of Zoology,  
University of Toronto, Canada

Why do passerines vary so much in the incidence of female song? Why do females in some species use "calls" and in others "song" to fulfil apparently similar functions?

Marcel Eens, University of Antwerp, Belgium

In a number of oscine and non-osine birds, females also sing. How is this reflected in their neuroanatomy, and what is the function of female song?

P. Galeotti,  
University of Pavia, Italy

Even in the temperate zone, however, females of some songbirds sing. The female Northern Cardinal routinely sings (Lemon & Chatfield 1971; Ritchison 1986; Yamaguchi 1998), with songs somewhat more variable in structure than the male's; she apparently can use song to communicate with her mate about parental duties at the nest (Halkin 1997). Females of a number of other species in the temperate zone sing less regularly, or at times other than the peak of the breeding season. Song Sparrow females sing in the fall, perhaps a manifestation of female/female competition (Arcese *et al.* 1988), and sedentary female White-crowned Sparrows sing in the fall and winter, perhaps to aid their mates in defending territories against floaters of both sexes (Baptista *et al.* 1993). Females might also use song to defend their own winter territories, as in Townsend's Solitaires (*Myadestes townsendi*—George 1987) and European Robins (*Erithacus rubecula*—Hoelzel 1986).

Females of species other than songbirds sing, too. Among columbiforms, females of many species sing (Cheng 1992; Baptista & Gaunt 1997b), as also do some female hummingbirds, such as the Blue-throated Hummingbird (*Lampornis clemenciae*—Ficken *et al.* 2000) and the Anna's Hummingbird (*Calypte anna*—Schuchmann 1979). Among the many duetting species listed by Farabaugh (1982) are many other female singers, too.

These examples of "female song" again raise the question of what is a "song". This dilemma is illustrated well by females of the genus *Thryothorus*. Females of some tropical species, such as the Buff-breasted Wren (*T. leucotis*), sing highly coordinated duets with their mates, with songs of the female and male both learned and equally complex, and with essentially equal investment in forebrain tissue for learning and controlling those songs (Farabaugh 1982; Brenowitz *et al.* 1985). In contrast, the female of the North American Carolina Wren (*T. ludovicianus*) uses a simple chatter to duet with her mate (e.g. Morton & Shalter 1977); this chatter is probably not learned and probably requires little, if any, investment in forebrain tissue (Nealen & Perkel 2000), but this simple chatter probably functions in much the same way as do the more complex, learned "songs" of her tropical relatives (most likely the joint defense of a year-round territory and mate—see below). The female Buff-breasted Wren clearly "sings", but we are inclined to label the simpler vocalization of the Carolina Wren "only a call", though for no truly objective reason. There is no obvious solution to this classification problem, of course, but none needs exist either, as use of the categories "call" and "song" is merely for our convenience and does not reflect any universal classification that the birds themselves use (see Spector 1994).

The functions of female song are poorly known (Langmore 1998). Because of the odd time of year at which some temperate-zone females sing, it was thought that they perhaps were singing only because of a hormone imbalance (Thorpe 1961). More recently, however, it has been realized that female song is under fine neuroendocrine control, as in the female European Robin, which has elevated testosterone levels as it defends a winter territory (Kriner & Schwabl 1991). Defense of territory or a mating situation may be one function of female song (e.g. Baptista *et al.* 1993). Female song in the impressive duetting species of the tropics probably also functions in joint defense of territory and in intrasexual defense of a mate (Hooker & Hooker 1969; Thorpe 1972; Hareus 1977b; for discussions of function, see also Todt *et al.* 1981; Farabaugh



1982). Especially fascinating is the song of the female Alpine Accentor (*Prunella collaris*), which is polygynandrous; females use their songs to attract males (Langmore *et al.* 1996), just as males of typically monogamous or polygynous species use their songs to attract females. With a growing interest in studying female song, not only in resident tropical species but also in migratory species outside the breeding season, we shall begin to understand better the role of female song.

Our focus on song production by females largely ignores another important field, that of song perception by females (Ratcliffe & Otter 1996). In most species, the female does not sing, yet it is she who chooses a mate, based in large part, we believe, on what a male sings. Just what does the non-singing female know about song, how does she know it, and to what use does she put that knowledge? How does she listen to her suitors? These are certainly some of the most crucial questions for understanding the evolution of song, yet we have so much to learn about how the female perceives her world.

### 3) The function(s) of song variation

Two particular features of song variation have been the object of frequent study. One is the number of different songs that an individual sings, and the other is how songs vary over geographic space. These two phenomena are largely a consequence of vocal learning, in that learning has permitted the development of large song repertoires and learning has resulted in micro-geographic song variation, or “dialects”. Although both phenomena result from song-learning, it should be stressed that one cannot therefore conclude that natural selection favored song-learning in some avian groups *so that* repertoire sizes could increase and dialects could form (see The evolution of sounds, below).

**Repertoire size.** Species differences in song repertoire sizes are considerable (for an attempt to standardize cross-species descriptions of songs, see Thompson *et al.* 1994; reviewed in Catchpole & Slater 1995). One of the simplest songs is that of the male Chipping Sparrow; his song consists of a repeated series of a single, brief syllable, and songs appear to vary only in overall duration because of different numbers of these repeated syllables that comprise each song (Borror 1959). Each song of a Swamp Sparrow (*Melospiza georgiana*) male is similarly simple, but careful listening reveals that the male first sings a series of songs based on one particular syllable, then a series based on another syllable, and so on, eventually revealing a repertoire of several different songs (3 or 4 is most typical; e.g. see Clark *et al.* 1987). An increasingly complex song repertoire is that of the Song Sparrow; males still tend to repeat a string of one particular kind of song before switching to another, but there are now roughly 5 to 14 different “song types”, each of which consists of several different phrases that vary in seemingly minor ways from rendition to rendition (Mulligan 1966; Searcy & Nowicki 1999). Song repertoires can be much larger, even huge. Western Marsh Wrens sing over 100 song types (review in Kroodsma & Verner 1997), Sedge Wrens 300-400 songs (Kroodsma, Liu *et al.* 1999), and Brown Thrashers over 1000 (Boughey & Thompson 1981).

Species also differ in how they present their song repertoires (e.g. Hartshorne 1956). Species with relatively few songs often sing with “eventual variety”, producing one song type several times before switching to another. Species with larger song repertoires often sing with “immediate variety”, such that successive songs are different from and more sharply contrasted with each other. Birds that sing with immediate variety often sing rapidly or continuously, with successive songs especially different from one another (Verner 1976; Kroodsma 1978b; Whitney 1981), as if eager to display their song repertoire. Understanding the relationship between the similarity of successive songs (variety, or versatility) and the rate of singing (or continuity) may help us understand the evolution of large song repertoires, as in the European thrushes (Ince & Slater 1985).

One important question to ask about these observations is whether or not our repertoire estimates mean anything to the birds themselves. Perhaps the best data are from Song Sparrows, the responses of which clearly show that what we identify as different song types (see Podos *et al.* 1992) are also distinctive to the birds, more so than the minor variations in renditions of each song type (Stoddard *et al.* 1992; Searcy *et al.* 1995). Other repertoire estimates seem reasonable, too, given that most are based on how the birds themselves learn and present their songs. What is often so impressive is that a songbird with hundreds of different songs in its repertoire (e.g. a Sedge Wren) can skillfully remember and reproduce the fine details of each song, so skillfully that sonagrams of thousands of songs unambiguously fall into a few hundred discrete categories. Songbirds are truly extraordinary in their ability to acquire

*What do daughters learn about song and singing, and when? And does this differ in species where females are active singers (like duetters) from those where females are (chiefly) listeners?*

Laurene Ratcliffe,  
Queen's University, Kingston, Canada

*Many songbird species exhibit patterns of song use that are extraordinarily intricate and complex. What are the functions of this structured complexity?*

Bruce E. Byers,  
University of Massachusetts, Amherst, USA

*Song repertoires, versions of single songs, and graded calls add variety to vocalizations of individuals. What does this variation communicate? How are others influenced?*

Bruce Falls,  
University of Toronto, Canada

*In many species of birds individuals produce many renditions of "the same" song or call. What advantage(s), if any, do such repertoires confer?*

Ken Yasukawa,  
Beloit College, Wisconsin, USA

*What is the real function of song repertoires?*

Satoshi Yamagishi,  
Kyoto University, Japan

*When territorial males countersing, what information are they exchanging and what are the proximal and ultimate consequences of this social interaction?*

Cindy Staicer,  
Dalhousie University, Halifax,  
Nova Scotia, Canada

*Vocal duelling among rivals is fascinating and complex in terms of the timing and structure of the exchanged songs. Do males say more than just "Stay away"?*

Dietmar Todt,  
Frei Universität, Berlin, Germany

(often by imitating) and store the details of these songs and in their ability to control the syrinx and vocal tract so that songs within a large repertoire are discrete, repeatable entities. All this is not to say, of course, that variation within each of these entities, or song types, is non-functional; the importance of this kind of variation has just received far less attention (Searcy & Nowicki 1999).

Even though we can classify sounds into discrete categories, we should not, of course, be fooled into thinking that the variation within these categories is meaningless. Although we may classify the simple *fee-bee-ee* of a Black-capped Chickadee as a single song type, for example, the male pitch shifts that one form over a considerable range of frequencies (Ratcliffe & Weisman 1985). In all species, different renditions of what we label the same song type or call may vary in subtle to not-so-subtle ways, and perhaps we should think of repertoires of variation embedded within each of the types that we have defined, such that we have hierarchies of repertoires.

What "good", then, are these repertoires of different songs? What purpose do they serve? In the following paragraphs, we consider a few possible answers.

One answer is that different songs can be used for different purposes, a phenomenon studied most thoroughly in the New World paruline warblers. In these species, one song (or group of songs) seems to be used primarily by unpaired males and in intersexual contexts after pairing; the other song (or group of songs) is used more in male-male countersinging, often in territorial conflicts (e.g. Ficken & Ficken 1967; Morse 1967, 1970; Lein 1978; Lemon *et al.* 1985; review in Spector 1992). A system in which songs have different functions can potentially convey more information; selection can also act independently on the two different song groups, creating, for example, geographically highly stereotyped songs in one group (female-attraction songs) or variable songs in the other (male-male interaction—see Byers 1996b; see Fig. 12 in next section; Staicer 1996a, 1996b).

For most species, however, it seems that song repertoires are not functionally structured. Of what use, then, is a large song repertoire for these species if all of the songs have the same meaning? What advantage does a male have in singing a repertoire? One possibility is that motivational information can be encoded in how the repertoire is presented. A male that sings several different songs in succession is typically more highly motivated than is a male that sings several renditions of the same song during such a time span, as has been demonstrated for a number of species (e.g. the Song Sparrow—Kramer & Lemon 1983; but for an apparent exception to this general rule in the Banded Wren *Thryothorus pleurostictus*, see Molles & Vehrencamp 1999). Under high motivation, then, there is an increased probability that the next song will be different, whether the male is interacting with another male (Kroodsma & Verner 1978) or with a female (Searcy & Yasukawa 1990). Indeed, evolution of large song repertoires in some species may have occurred under ecological or social circumstances in which competition for resources was continually high, as in dense populations, where competing males interact frequently and intensely (Kroodsma 1999).

Additional information can be encoded during presentation of a song repertoire if males learn their songs from each other. With "shared" repertoires, males can select particular songs so that they "match" each other during a countersinging performance (e.g. Northern Cardinal—Lemon 1968; Yellowhammer *Emberiza citrinella*—Hansen 1981; Common Nightingale—Todt 1981; or Western Meadowlark *Sturnella neglecta*—Falls 1985). It is as if a male names his opponent in a song duel (Armstrong 1963), and this "matched countersinging" has now been described for many songbird species (e.g. Krebs *et al.* 1981; see Whitney 1990 for an apparent example of how birds might avoid matching; see Beecher *et al.* 2000 for a special example of "repertoire matching" instead of "song-type matching"). These behavioral exchanges reach a feverish pitch in a species like the Marsh Wren of western North America (Fig. 11; Verner 1976): each male has 100–200 songs in his repertoire, and successive songs are different, so that a male must decide every few seconds which particular song he will sing next. He can choose to match a song that one of his neighbors just sang, or he can advance to the song that he anticipates next from a neighbor, or he can choose other songs, as if ignoring his singing neighbor. These escalated styles of interaction have evolved in a few other species, too, such as the Common Nightingale (Hultsch & Todt 1986; Todt & Hultsch 1996). The potential for conveying information in these countersinging duels is truly immense. Such exchanges, for example, could provide information about male dominance hierarchies or age, which would be relevant not only for territorial defense but also for prospecting females which eavesdrop on how males interact (e.g. Kroodsma 1979). These kinds of exchanges alone could have favored the evolution of large song repertoires in some species.

The size of a song repertoire might also be an honest indicator of the singer's overall health (e.g. Nowicki, Peters & Podos 1998). In Sedge Warblers, a male's parasite load is negatively related to the size of his song repertoire and to his provisioning



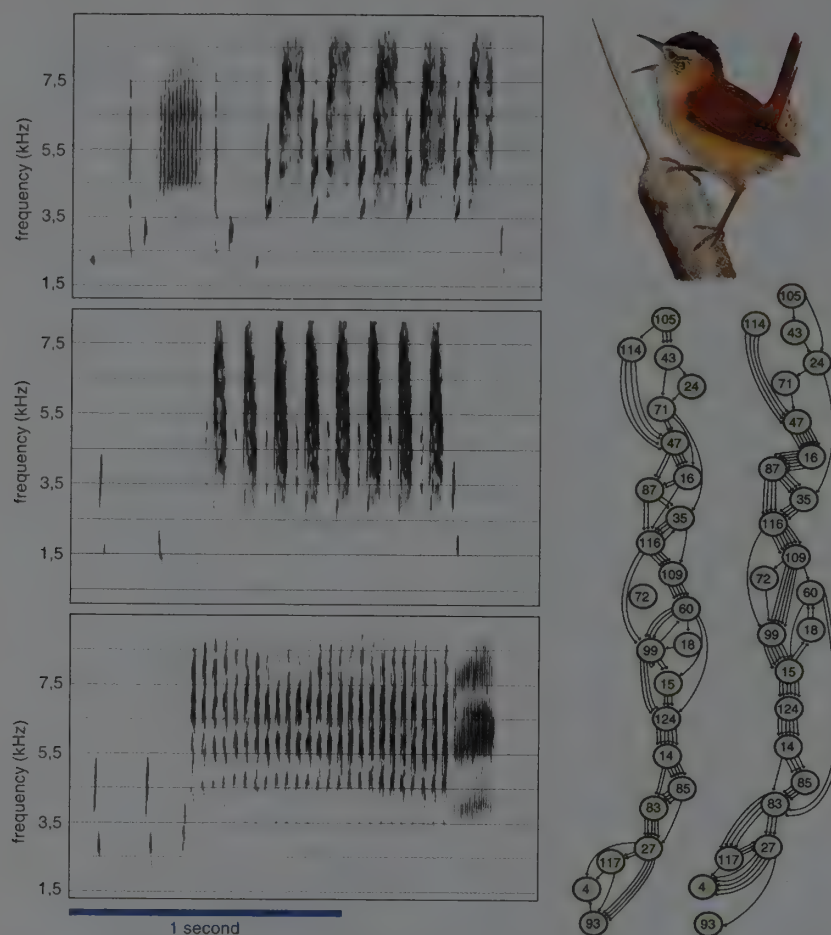


Figure 11. Marsh Wren males duel with their large repertoires. Illustrated are 3 representative song types from a repertoire of more than 100 song types, and representative transition flow diagrams of song types from two males at Turnbull National Wildlife Refuge, Washington, USA. Each circled number in the flow diagram represents a different song type, and each arrow represents one transition that the male sang, with multiple arrows showing favorite sequences. Neighboring males learn the song sequences from each other, and when countersinging can choose to reply with the same type, to advance to the next song type expected in the sequence, or to ignore the neighbor altogether (after Verner 1976).

rate at the nest, so a female could use repertoire size as a cue to choosing a healthy mating partner (Buchanan *et al.* 1999). The number of songs that a Marsh Wren can learn appears to be related to the size of his song nuclei, which may be an honest indicator of his health (Brenowitz *et al.* 1995). In Bewick's Wrens, song repertoire size may be correlated with hatching date, and a young male hatching early in a breeding season may be healthier and have many advantages over young males hatching later in the season (Kroodsmma 1974). A similar correlation between repertoire size and hatching date is found in Brown-headed Cowbirds (S. I. Rothstein, unpublished data). Indeed, song repertoire size is strongly correlated with longevity as well as with annual and lifetime reproductive success in one population of Song Sparrows (Hiebert *et al.* 1989), and repertoire size in Great Tits is also highly correlated with fitness (McGregor *et al.* 1981; Lambrechts & Dhondt 1986). The mechanisms by which repertoire size might influence success are unknown, however. One possibility is that males use larger repertoires directly to impress females or to acquire resources (e.g. a territory) critical for reproductive success; another possibility, of course, is that repertoire size is simply correlated with other male traits that enable success.

All of this fascination with large song repertoires must be tempered with a discussion of why so many species have such small song repertoires, or no repertoire at all, i.e. a single song type. Given our belief in the power of natural selection, these species cannot be dismissed as inferior and incapable of responding to what we often think of as ubiquitous selection pressures for large repertoires; rather, for some reasons, these species must encounter different forms of selection for vocal variability, with necessary information (e.g. for female choice) encoded in one or a few song types. Evidence for selection limiting repertoire size comes from a number of species in which males practise much larger song repertoires than they eventually produce, showing that the brain and motor apparatus are certainly capable of singing larger song repertoires (Marler & Peters 1982). Song repertoires can be behaviorally constrained in individuals and in populations, as illustrated by the Black-capped Chickadee. From British Columbia to Nova Scotia, across the North American continent, male chickadees sing a highly stereotyped *fee-bee-ee*, a single song form that varies in frequency (Horn *et al.* 1992). In the laboratory, however, birds from these same populations achieve song repertoires of up to 4 different types, and groups isolated from each other form

*Females prefer males with more complex songs, but how does the structure of the song reflect male quality?*

Clive K. Catchpole,  
University of London, UK



different dialects, just as repertoires and dialects form in certain isolated populations of this species (review in Kroodsma, Byers *et al.* 1999). Why repertoires (and interpopulation variability) are so constrained in some chickadee populations is unknown, though social factors involving female choice of mates is a likely suspect (Otter *et al.* 1998).

**Geographic variation.** How songs vary over geographic space also varies considerably among species. Among species that do not learn their songs, such as New World flycatchers (see above), geographic variation is low (Lanyon 1978); songs are “hard-wired”, and populations of individuals with similar genotypes have similar songs. Intraspecific song variation is also low in shorebirds, which likely do not learn their songs (Miller 1996). Indeed, if populational differences in song become too great among these non-learners, the populations are often considered to be separate species (Isler *et al.* 1997).

When species do learn their songs, micro-geographic song variation often occurs, in the form of song “dialects”. Such dialects occur in a host of song-learning species, such as the sunbirds of Africa (Grimes 1974; Payne 1978b), the Winter Wren (Catchpole & Rowell 1993), Redwings (*Turdus iliacus*—Bjerke & Bjerke 1981), Corn Buntings (*Miliaria calandra*—McGregor 1980; McGregor & Thompson 1988), Neotropical hummingbirds (Gaunt *et al.* 1994), House Finches in North America (*Carpodacus mexicanus*—Mundinger 1975), Saddlebacks in New Zealand (Jenkins 1978), and, indeed, in almost every songbird that has been studied carefully (Krebs & Kroodsma 1980).

The pattern of micro-geographic variation differs among species, and even among closely related species and among populations of the same species. *Zonotrichia* sparrows illustrate these patterns well, with sharp dialect boundaries occurring in the White-crowned Sparrows in the coastal chaparral of California (Marler & Tamura 1962; Baptista 1975) but not in Alaska (DeWolfe *et al.* 1974), perhaps a consequence of the short season for vocal development in Alaska (Nelson 1999). The congeneric Rufous-collared Sparrow of Central and South America has sharp dialect boundaries (Nottebohm 1969), but the North American White-throated Sparrow does not (Lemon & Harris 1974). Other contrasting patterns occur among populations of *Melospiza* sparrows (Searcy & Nowicki 1999), *Cistothorus* wrens, and *Pipilo* towhees (review in Kroodsma 1999). The literature on how bird songs vary over geographic space is truly immense (see reviews in Krebs & Kroodsma 1980; Catchpole & Slater 1995), and documenting how these song dialects occur (Lemon 1975) has certainly been a passion among field biologists.

Showing how songs change over geographic space is much easier than determining why they change in the way they do. Any proposed explanations should, of course, focus on advantages that individuals might have in acquiring songs like or unlike those of other individuals, as the extent of geographic variation in song is a consequence of evolutionary “choices” made at the level of the individual.

One possible influence on song could be the habitat in which song is used (Hansen 1979). Habitats do influence which types of sound transmit best (Wiley 1991), and, as habitats vary geographically, so too might song vary geographically (Bowman 1979; Gish & Morton 1981). Supporting data for this hypothesis come primarily from the Rufous-collared Sparrow (e.g. Nottebohm 1969; Handford & Loughheed 1991; Loughheed & Handford 1992). A match between song and habitat almost certainly does not, however, explain why the fine structure of songs changes at abrupt dialect boundaries in continuous habitat of other species, as with the White-crowned Sparrow in California chaparral.

For *Zonotrichia* sparrows, another hypothesis has been proposed, the genetic adaptation hypothesis (Nottebohm 1972). Perhaps local birds that breed together maintain co-adapted gene complexes that favor local adaptations, and learning a local song dialect might help to maintain an optimal level of such inbreeding (e.g. Bateson 1978). This hypothesis predicts that young males and females will be influenced by their father and learn the songs of their natal dialect, that they will preferentially settle in and breed in the natal-dialect area, that dialect boundaries will inhibit dispersal, and that birds of adjacent dialects will differ genetically. Evidence supports some or all of these predictions, depending on who evaluates the data, and this issue was hotly debated in the mid-1980's (Petrinovich *et al.* 1981; Baker & Cunningham 1985; see review in Catchpole & Slater 1995). Although increasing evidence for several species shows that young birds can and do disperse to localities where songs are different from their father's (e.g. Payne & Payne 1997), we really do not know for any species the extent to which early experience with the song of the father influences the destiny of his offspring (see Grant & Grant 1996 for a possible example of sons learning the father's song and females mating with males which have songs unlike that of their

*From tinamous to tyrant-flycatchers, vocalizations often vary geographically in species that supposedly do not learn. Have we underestimated 1) the true species diversity of these groups or 2) the number of groups in which learning occurs?*

F. Gary Stiles,  
Universidad Nacional de Colombia

*Do dialects form during founder events, and dialect areas grow with population expansion? Could that idea be tested after the recent large wildfires in the western United States?*

Myron C. Baker,  
Colorado State University, Fort Collins, USA

*What good are “song dialects”? Do they influence mating decisions, or are they simply an epiphenomenon of the song-learning process?*

Marty Morton,  
University of Alaska, Fairbanks, USA

*Song structure in many songbird taxa fits environmental-acoustic expectations, yet other taxa do not show this. How do their use and context of vocal signals differ?*

Paul Handford,  
University of Western Ontario, London, Canada

father). Obtaining answers to these important questions about dispersal and mating patterns in nature is simply very difficult.

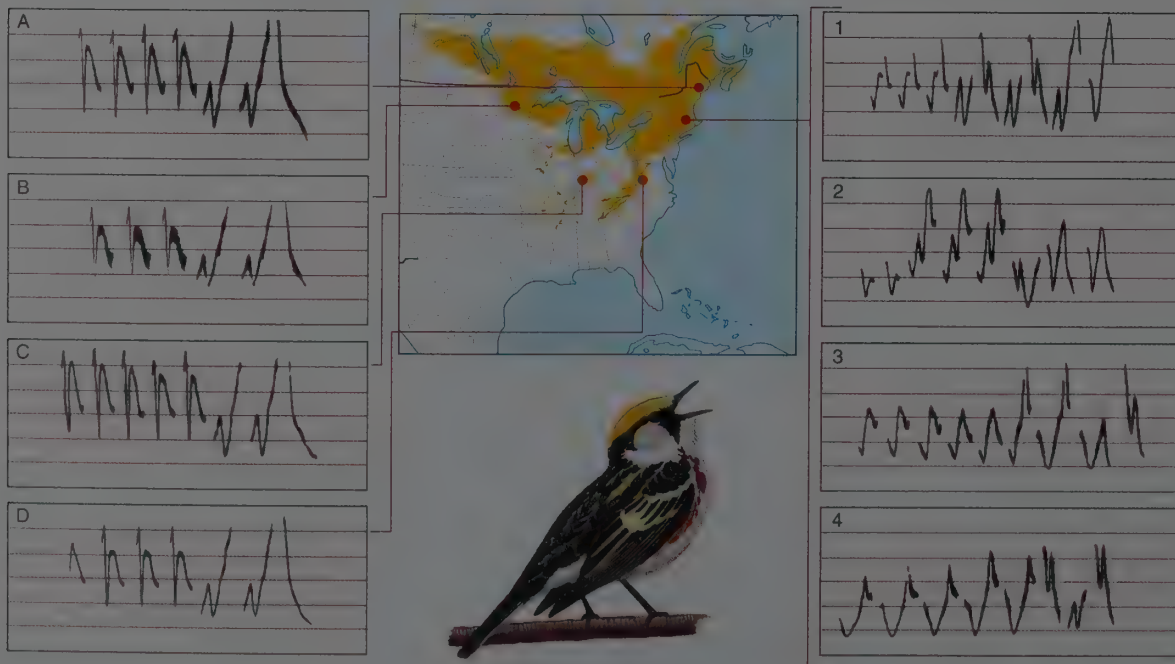
Another explanation for why songs vary over space has been attributed to "social adaptation". This hypothesis proposes that a young bird recruited into a local breeding population will have some advantage if he learns the local songs. This hypothesis is essentially a truism, given that young birds typically do learn local songs where they breed, so the real quest is to determine what the advantage might be. One possibility is that birds that use local songs convey their membership in the community (Feeles 1977); because learning the songs takes time or effort, a male singing the local songs indicates honestly his tenure within the community, and his songs might thus be a cue to prospecting females (Rothstein & Fleischer 1987). Perhaps learning a song from a dominant neighbor enables a young male to obtain an adjacent territory, especially if the dominant male has opportunities for extra-pair fertilizations in the mate of the younger male (Greene *et al.* 2000). A contrasting (though perhaps less likely?) explanation is that learning the song of a dominant, older male might convey some benefits to a younger male if the younger male might then occasionally be mistaken for the older (Payne 1981); the benefits result, then, from deception, not honesty.

These three hypotheses aside, we almost certainly can use existing patterns in geographic song variation to inform us as to function. Consider, for example, the functionally structured song repertoires of the Chestnut-sided Warbler (Fig. 12; Byers 1995, 1996a, 1996b). The songs used in male-male interaction are shared only by immediate neighbors; these songs must be learned at the site where a young male will breed, because the local neighborhood is the sphere of influence for these songs. In contrast, the limited repertoire of four different songs used to attract females is highly stereotyped, and each song occurs throughout the geographic range of the species; these songs are thus highly conservative, both temporally and geographically, as a male apparently strives to attract a female from any geographic origin. For these two song systems, the sphere of expected influence for a song matches the pattern of geographic variation.

Another example is provided by the *Cistothorus* wrens. A male Sedge Wren in North America improvises a large repertoire of species-typical songs, and songs of neighboring males seem to be no more alike than songs of distant males; the apparently uniform distribution of song characteristics throughout the geographic range enables a male to communicate with any male or female that might be encountered in the semi-nomadic lifestyle of this species. Strikingly different is the pattern of geographic song variation among resident male Marsh Wrens of western North America. A young male imitates the songs of his adult neighbors precisely, and they engage in highly coordinated, matched-countersinging duels (Verner 1976); neighboring males know each other, as they reside next to each other over a lifetime, and the sphere of influence of these particular learned songs would be expected to be more local.

A corollary of this approach is that some patterns of geographic variation will occur by chance, because at increasing geographic distances selection for sharing of

Figure 12. When different songs in a male's repertoire have different functions, selection can act on the properties of each independently, producing, as illustrated here, great differences in geographic variation. Songs that Chestnut-sided Warblers seem to use primarily with females are highly conservative over space and time, and males throughout the breeding range of the species share these songs, as shown by examples A-D recorded from 1957 to 1990. In contrast, songs used in male-male interactions are shared only by immediate, interacting neighbors, and birds only a few territories away have different songs. Examples 1-4, recorded in 1990, are from four different neighborhoods, and are but a few of the hundreds of different song types found in a 1 km<sup>2</sup> area in western Massachusetts (see Byers 1995, 1996a, 1996b).





Has vocal learning facilitated speciation in birds?

Douglas A. Nelson,  
Ohio State University, Columbus, USA

How does song-learning affect mate choice and how does it result in the evolution of new species of birds?

Robert B. Payne,  
University of Michigan, Ann Arbor, USA

What will efforts to understand the information encoded in avian signals reveal about the cognitive processes that underpin communication?

Christopher S. Evans,  
Macquarie University, Sydney, Australia

Should the emerging intricacies of the two-voice phenomenon (unique to birds) and discrete brain nuclei (in contrast to diffuse brain areas in mammals) lead us to rethink the parallels between human speech and bird song?

Sandra L. L. Gaunt,  
Ohio State University, Columbus, USA

Could someone explain the paradox of structured cawing in crows? Why do the individuals of a group sometimes seem to call in distinct "voices", and yet on other occasions shift dramatically from voice to voice?

Nick Thompson,  
Clark University, Worcester,  
Massachusetts, USA

vocal characters will diminish. Sharing of vocal characters tends to decline rapidly over distance in resident populations, and less rapidly in populations that are migratory or less site-faithful (e.g. Ewert & Kroodsma 1994). At some distance, then, beyond the expected sphere of influence of songs, i.e. in the absence of selection for vocal similarities, accumulations of copy errors or improvisations may lead to differences in songs (Searcy & Nowicki 1999). Some features of songs could remain constant over large geographic distances, of course, even in the absence of selection, such as when some aspect of song structure is genetically inherited and phylogenetically conserved (e.g. Martens 1996); similarity of song characters over larger stretches of geographic space might then reveal past spheres of influence, or the phylogenetic history of the larger group.

A final topic that begs for discussion is that of cultural evolution (Lynch 1996; Payne 1996). Learned songs within populations are cultural traditions, and these learned components (memes) vary not only over space but also over time. Populations of song characters change over time because of relationships between song tutors and their pupils and because of how and from whom an individual male chooses his particular songs to learn. For Indigo Buntings, the cultural survival of a song learned by a young male is estimated to be about three times the survival rate of the male himself (half-life survival of song is 4.2 years, that of male 1.3 years; Payne 1996). A special case of cultural evolution was described by Trainer (1989): males within a colony of Yellow-rumped Caciques (*Cacicus cela*) all have the same songs (Feeckes 1977), but songs change during the lifetime of individual singers, so that males must constantly listen to each other and adjust their songs accordingly (much as happens within entire populations of humpback whales *Megaptera novaeangliae*—Payne *et al.* 1983). Common Starlings, too, adjust to different social situations by modifying their songs, so that songs within a colony change over time (Adret-Hausberger 1986; Adret-Hausberger *et al.* 1990; Hausberger 1997). Another example of this kind of cultural evolution is found among the suboscine Three-wattled Bellbirds (*Procnias tricarunculata*) in Costa Rica, where males throughout each of two dialects modify their songs over time to match each other (Kroodsma *et al.* 2001). How these various learned song traditions might influence genetic population structure, i.e. the coevolution of cultural and genetic traits, and how they might affect speciation are especially fascinating areas of inquiry (Lachlan & Slater 1999; see above).

#### 4) Vocal variation and intelligence

In all of these discussions of calls, songs, and how and why they vary, we often think of birds as robots, with males and females responding in some reflex-like fashion to sounds in their environment. This thinking on our part is reinforced by the seemingly "stupid" behavior of birds in some circumstances (such as repeated attacking of a self-image in a window), but a surge of interest in animal cognition (e.g. Balda *et al.* 1998) is helping us take another look at the mental abilities of birds. Some communicative studies of birds reveal capabilities that are truly extraordinary, suggesting that these birds use considerable mental capacities when interacting with other birds (e.g. Hausberger 1993; Kroodsma & Byers 1998; Smith 1998).

One suggestion of "intelligence" in songbirds derives from their similarity to us and our immodest opinions of ourselves. We learn to speak, and these songbirds learn to sing; we babble as we practise, as do the young birds, although for them the babbling is called "subsong". Both humans and songbirds must be able to hear in order to learn, and in both groups the learning leads to vocal dialects. Brains of both are lateralized for sound learning and production, too. Some warblers seem to learn not only their songs but also the contexts in which to use them (Kroodsma 1988b), which is what we do with our words, too. These oft-cited parallels between human speech and bird song (Marler 1970a) need have no bearing on intelligence in the birds, of course, but the similarities do force us to think about what intelligence is, and how we differ, or how much we differ, especially given the seeming absence of similar vocal learning among chimpanzees and other primates (Marshall *et al.* 1999; Mitani *et al.* 1999).

One particular group of birds, the corvids, is widely regarded as intelligent (e.g. Heinrich 1989, 1995), but we know so little of their vocal behavior (e.g. see Thompson 1982). Crows, ravens and jays do not sing in the usual sense, but they have complex vocal repertoires (Hardy 1967; Elowson & Hailman 1991). Ravens in particular are renowned for their cunning as well as their diverse repertoire of squawks, rattles, chortles, yells, and so much more. As we find the courage to tackle the complex vocal communication systems of these corvids, we shall surely learn more about the minds of these intelligent creatures.



Pepperberg's (1999) recent review of her studies with Alex, the African Grey Parrot (*Psittacus erithacus*), certainly force us to realize that not all birds are the creatures of instinct that we once thought they were. As Alex competes for attention with two humans, he learns how to use his human language in appropriate contexts (a technique developed by Todt 1975). By speaking in a "tongue" that we humans can understand, Alex has revealed that he knows far more about his world than we would have given him credit for if he had vocalized only in parrotese. He can identify numerous items in his environment, count them, and can request or refuse them. He can identify the color, shape or make-up ("matter") of an item, and can group items by these three categories. More impressively, when asked what a group of items has in common, he can tell whether it is the shape, the color, or the matter from which they are made. He knows the concept of "none", too, because when asked what numerous dissimilar items have in common, he responds with the word "none". These abilities are revealed in a highly artificial laboratory environment with human social companions, but each grey parrot in nature must also have these same abilities. Just how might those abilities be used in nature? What kind of information is really conveyed between parrots with what seems like a series of amorphous, meaningless squawks? We do not know, but Pepperberg's work with Alex has clearly encouraged us to re-think the minds of the birds that we work with.

## The evolution of sounds

What we know about how and why avian sounds have changed over evolutionary time is inferred largely from our studies of current song function among a diversity of species. A danger lurks here, however, because one cannot assume that current functions or characteristics of a vocalization necessarily reveal the reasons for origin of that behavior (Gould & Lewontin 1979). For example, although song-learning enables large song repertoires and regional dialects, we cannot assume that selection for repertoires or dialects favored the origin of vocal learning.

One big question to which we would like an answer is, of course, "How or why did song evolve?" Because of presumed current functions, we often assume that complex male song arose via sexual selection to impress females, and the literature is replete with studies and theory about sexual selection and how song is used to impress other individuals. This pathway certainly seems plausible; a recent study of Zebra Finches, for example, showed that females preferred even longer and more complex songs than males routinely deliver (Neubauer 1999). The best we can do on evolutionary questions, however, is to generate plausible explanations, but we should also remind ourselves that our "song category" is highly artificial (Spector 1994). In sexual selection theory, we think of functional definitions of song, but then we should think more broadly, in terms of what behaviors (or other features, such as feather structures) function to impress members of the opposite sex. We then realize that all species must have a "song", because mate choice occurs in all species, but that the functional "song" of some species might not be vocal.

Another big question is "Why did vocal learning evolve?" Learning involves risks, and many examples of interspecific song-learning "mistakes" have been documented (e.g. Baptista & Morton 1981). Few hints are offered by surveying the distribution of vocal learning among bird groups. Songbirds learn their songs, of course, but members of their sister suborder within the order Passeriformes had been thought not to (Kroodsmas 1988a). New data now show, however, that bellbirds (*Procnias* spp.), close relatives of the flycatchers, do learn their songs, thus confirming Snow's earlier conclusions (Snow 1977; Kroodsmas *et al.* 2001). Other vocal learners include the parrots (Farabaugh & Dooling 1996; Wright 1996), certain hummingbirds (Snow 1968; Wiley 1971; Baptista & Schuchmann 1990), and probably a duck (Musk Duck *Biziura lobata*—McCracken 1999), with hints of some subtle degree of vocal learning in a few other avian groups (Sparling 1979). Explanations as to why vocal learning evolved range from protecting the inner ear during loud vocalizing (Nottebohm 1991) to an arms race over "ranging" (i.e. using sounds to estimate distance of conspecifics—Morton 1996b), but no current explanations are satisfactory.

As this question is pondered, it is important to realize that social learning can involve not only imitating the signal but also learning how to use that signal in appropriate social contexts (e.g. West *et al.* 1997; Janik & Slater 2000), and distinguishing among the different forms of learning will help us understand more clearly their respective origins. We should also remember the surprising conclusion of the model developed by Lachlan & Slater (1999), that once song-learning has evolved in a lineage, it might be maintained by an "evolutionary trap", and reverting to non-learned signals might be

*Why do parrots have such a relatively simple vocal repertoire yet have such an enormous capacity for learning new sounds?*

Stuart Taylor,  
University of Natal, Pietermaritzburg, South Africa

*Given the intelligence and vocal plasticity of Grey Parrots as demonstrated in laboratory tasks, to what use might these abilities be put in the wild?*

Irene M. Pepperberg,  
Massachusetts Institute of Technology,  
Cambridge, USA

*Given family-level similarities in calls, songs and singing behaviors, can we both identify homologies and make ecological sense of variation within groups?*

David A. Spector,  
Central Connecticut State University, USA

*Which component of male courtship behavior, visual (dancing) or auditory (song), is more important for mate choice by female estrildid finches?*

Maki Ikebuchi,  
Chiba University, Japan

*What are the selective forces that led to the evolution and maintenance of song-learning in some groups of birds but not in others?*

Peter J. B. Slater,  
University of St. Andrews, Scotland

*Vocal learning evolved among just a few groups of birds: parrots, hummingbirds, and songbirds. Exactly what selective forces led to learning in these groups?*

Karl-L. Schuchmann,  
University of Bonn, Germany

*Shorebirds, rails, cranes, hawks, etc. are long-lived with complex social relationships, but have relatively simple, non-learned vocalizations. Do the communication systems of such species differ in fundamental ways from those of songbirds?*

Edward H. Miller,  
Memorial University of Newfoundland,  
St. Johns, Canada

*If song-learning is one reason why the oscine passerines are so successful evolutionarily, why do non-learning suboscines (e.g. tyrant-flycatchers) have life histories so similar to those of oscines?*

M. Ross Lein,  
University of Calgary, Alberta, Canada

*Do birds like to hear themselves sing? Is this reinforcement greater for birds (oscines, parrots, hummingbirds) that learn their song? Do they enjoy matching a model?*

Fernando Nottebohm,  
Rockefeller University, New York, USA

*Did learned vocalizations evolve because they facilitate assessment of individuals and, if so, was this due to innate or learned preferences for elaborate vocalizations and large repertoires?*

Steve Rothstein,  
University of California, Santa Barbara, USA

*Are large, complex vocal repertoires primitive character states in many lineages? Are simpler song repertoires derived traits associated with social monogamy?*

Juan Francisco Ornelas,  
Instituto de Ecología, AC, México

*Will tropical-forest fragmentation decrease the diversity of vocal repertoires of forest species?*

Julio Sánchez,  
Museo Nacional, San Jose, Costa Rica

impossible. Whatever the evolutionary patterns of vocal learning, our knowledge of the world is far from complete, and additional surveys of poorly known groups are needed, especially in the New and Old World tropics (Kroodsma, Viellard & Stiles 1996).

Inferences about the evolution of male song characteristics are sometimes made from correlations between current behavior and ecological context. This comparative approach suggests that large song repertoires develop when songbird males compete intensely for mates or territories, as in dense populations (review in Kroodsma 1999). In none of the studies suggesting this correlation (Catchpole 1980; Kroodsma 1983; Catchpole & McGregor 1985), however, is the phylogeny of the birds known, so that identifying independent evolutionary events is impossible in reconstructing evolutionary pathways. Ideally, one would want to know phylogenies and even to estimate how males or females would respond to ancestral vocalizations (Ryan & Rand 1995). More studies like Irwin's (1990) are needed, in which she mapped repertoire size onto a phylogeny of New World blackbirds and concluded that directional selection cannot explain the evolution of different repertoire sizes among these species.

The evolution of singing behaviors can also be inferred from patterns of geographic variation. The Greenish Warbler (*Phylloscopus trochiloides*) has relatively simple songs in the Himalayas, but in two independent radiations extending to the north its song becomes more complex. Irwin (2000: 998) concludes that "parallel south-to-north ecological gradients have caused a greater intensity of sexual selection on song in northern populations and that the stochastic effects of sexual selection have led to divergence in song structure."

Because vocalizations have diverged in different avian lineages, sounds can be used as characters in systematics (Lanyon 1969; Payne 1986; Miller *et al.* 1988; Martens 1996; Miller 1996). Vocalizations that are not learned, such as most call notes or songs of suboscines, are more conservative characters and therefore best track phylogenies. The non-learned song differences between the Alder and Willow Flycatchers (*Empidonax alnorum* and *E. traillii*), two sibling species, were used to identify them as species (Stein 1958), just as current studies of non-learned suboscine or non-passerine songs in the Neotropics are revealing additional species (Fig. 13; Isler *et al.* 1997, 1998; Robbins & Stiles 1999). Non-learned calls also identify evolutionary units, as in Winter Wrens, in which eastern and western populations have markedly different call notes (Garrett & Dunn 1998).

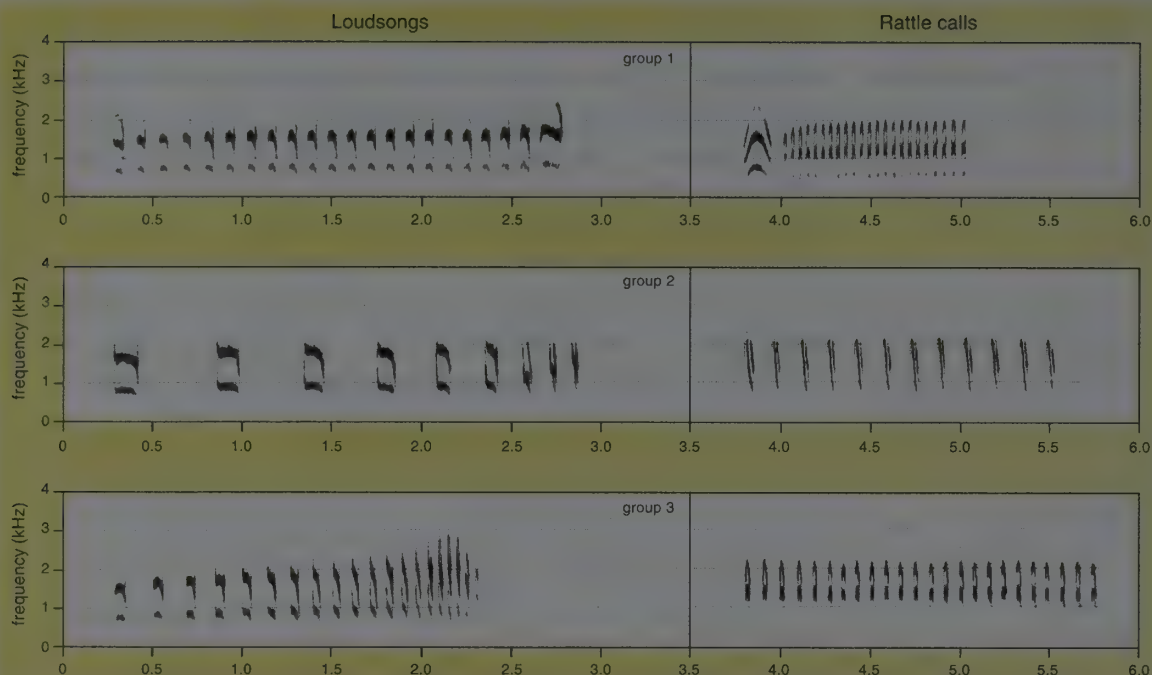
Learned vocalizations can also offer clues to phylogenetic histories, but interpreting the data requires more caution. In North America, for example, the learned songs of eastern and western populations of the Marsh Wren are unmistakably different, even though a male is capable of learning songs of either tradition (Kroodsma & Canady 1985); characteristics of the learned songs have been preserved over space and time, thus preserving information about phylogeny. Similarly, sympatric Red Crossbills (*Loxia curvirostra*) with different learned calls appear to mate assortatively, so that different breeding populations can be identified by their call notes alone (Groth 1993). Sometimes phylogenetic information among learned vocalizations can be found in traits that are the more genetically based (e.g. see Baptista 1996). The ability to learn song repertoires may differ genetically among populations, for example, such that the number of songs a male sings, but not the qualities of the songs themselves, can provide a useful systematic character (Kroodsma & Canady 1985); other traits, too, may be relatively conservative because their variability is limited by morphology (Podos 1996, 1997, 2000).

## Looking forward

We hope that this foreword begins to reveal the extraordinary world of bird sounds and the passions of those who thrive on it. The thriving and passion occur at all levels, of course, from the poets who just want to listen and connect with and celebrate our Planet Earth, to the neurobiologists who search for how songs may be stored in the brain's neurons. In every scientist who studies bird song, however, there lies a poet, too, as all who are privileged to know this world of bird sound are deeply affected by it, well beyond whatever the biological significance of our discoveries might be. Epitomizing this inevitable multi-faceted effect that bird sounds have on us was Luis Baptista, the poet, philosopher, musician, biologist, and all-around enthusiast. It is his enthusiasm and outright joy of knowing the beauty of bird sounds, at all levels, that this foreword celebrates.

And where do we go from here? In so many different directions! Some of our initial concerns must be about conservation of birds, to preserve avian biodiversity on this planet. Use of bird sounds is crucial here (Baptista & Gaunt 1997a), not only to





help determine the units of biodiversity we wish to preserve (e.g. Isler *et al.* 1997), but to help survey critical habitats (Parker 1991) or to monitor the number of migrants passing overhead (Evans 1994). Sound playback can be used not only to locate and identify individuals or populations, but also to help re-establish breeding populations, a technique used successfully with colonial seabirds (Kress 1992). Sound can also be used as a tool to identify individuals, which is valuable if catching or handling members of an endangered population would be detrimental (Telford 1993).

An increasingly important role in conservation (as well as in other studies of bird sound) is being played by the major archives of bird sounds (Kroodsma, Budney *et al.* 1996), as the sounds archived there can aid studies of all kinds, from conservation to systematics to general behavior. A sampling of those archives would include the Library of Natural Sounds at the Cornell Laboratory of Ornithology, Ithaca, New York; the Wildlife Section of the National Sound Archive at The British Library in London; the Borror Laboratory of Bioacoustics at Ohio State University; the Bioacoustics Archives and Library at the Florida Museum of Natural History in Gainesville, Florida; the Australian National Collection of bird sound recordings at the National Film and Sound Archive, Canberra; the Fitzpatrick Bird Communication Library at the Transvaal Museum, Pretoria, South Africa; the Vepintsev Phonotheke of Animal Voices in Puschino, Russia; the Phonotek of Animal Voices, Lomonosov State University, Moscow, Russia; the Tierstimmenarchiv at Humboldt University, Berlin; the Fonoteca, Museu de Zoologia in Barcelona, Spain; the Laboratorio de Sonidos Naturales, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; and the sound archive at the Universidade Estadual de Campinas, Brazil. As these archives grow, they become increasingly valuable in many ways, and amateur as well as professional biologists are encouraged to contribute much-needed recordings of bird sounds to these archives (Bradbury *et al.* 1999).

Beyond conservation, the possibilities are limitless, as revealed by the diversity of questions that have been contributed to this foreword by leading bioacousticians throughout the world. So much remains to be learned, from how the syrinx works, to how songs are stored and controlled in the brain, to why birds acquire and use their sounds the way they do, to how and why sounds have changed over evolutionary time. We hope that the collective passions of those who study bird sounds, not the least of which were those of the late Luis Baptista, will serve as a welcoming invitation to others who would join us in the quest to understand what bird sound is all about.

**Acknowledgements:** Thank you, to friends and colleagues of Luis Baptista who contributed your questions as a tribute to Luis; to Eliot Brenowitz, Bruce Byers, Toby Gaunt, Frank Gill, Mort and Phylis Isler, Wan-chun Liu, Irene Pepperberg and William Munoz, Kathleen Berge and Helen Horblit, and David Sibley for your help with the figures; to

Figure 13. Bird sounds can be used not only to identify known species but also to identify new species. Especially useful in avian systematics are the non-learned "conservative" sounds, which have been used to help sort out how many species of the subspecies Slaty Antshrikes (the *Thamnophtilus punctatus* complex) occur from Belize to south-eastern Brazil. Shown here are sonograms of the highly distinctive "loudsongs" and "rattles" for three groups from this antshrike complex, and each group probably warrants species status (from Isler *et al.* 1997).



Will our children's grandchildren be able to enjoy listening to a living nightingale, a lark, or a warbler?

Richard Rant,  
The British Library National Sound Archive,  
London

A goal: That amateur and professional bioacousticians fully realize the immense value of their audio recordings by archiving them for use by others.

Greg Budney,  
Library of Natural Sounds,  
Cornell Laboratory of Ornithology, Ithaca, USA



*If we could teach the world  
the Magic in a singing bird and  
the Ecstasy in listening,  
could we help save this dying planet?*

Don Kroodsmas,  
University of Massachusetts, Amherst, USA

HBW editors Andy Elliott and Josep del Hoyo and your staff for a class act; to Greg Budney, Bruce Byers, Eben Goodale, Elijah Goodwin, Henrike Hultsche, Steve Johnson, Wan-chun Liu, Jeff Podos, Gary Stiles, Nick Thompson and, especially, David Spector for your help on the manuscript; to Sandy Gaunt for helping from A to Z; to the National Science Foundation for research support (IBN-9408520); and a special thanks to those around the world who have helped make the study of bird sounds a lifetime passion for so many of us. My apologies to those who would have liked to participate in this tribute but whom I overlooked or could not reach in time.

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## *Introduction to Volume 6*

Since completing Volume 5 of HBW, we have come to an important decision which will affect the whole of the rest of the project. We consider that is important to keep our readers fully informed of all developments, and so take this opportunity to offer you a brief explanation.

We always realized that Volume 6, as originally planned (Mousebirds to Woodpeckers), promised to be one of the most spectacular volumes in the series, with so many exciting and spectacular families involved. The number of families, 18, we knew to be fairly high, but considerably lower than the 27 of Volume 1 and the 30 of Volume 3. Another consideration was that we always felt that these were families for which we would want to publish particularly comprehensive selections of photos.

However, when this volume finally began to take shape, we found that our calculations had been thrown way out. First of all, with so much interesting material for discussion, all of the family texts were running long, and we could see that it was going to be difficult to “edit short” without losing a good deal of useful and interesting material. Second, the number of striking photos proved far higher than we had anticipated, even though we were already allowing for a strong tendency this way. When making the photo selection for the volume, we consistently shot way over the top of our highest estimates, and felt that we could not reduce the final selections any further without losing a great deal of spectacular photos. Third, though spread out over a much longer period, the number of plates for the volume also mushroomed from an original (highly unrealistic) estimate of 60+ up to a total of very nearly 100, a far cry from the 50 of Volume 1, the 60 of Volume 2, etc.

Various factors have played their parts in the major growth seen throughout the series as a whole since the original planning. For example, the average length of the texts, especially the species accounts, has grown considerably since Volume 1, mainly because of the vast amount of ornithological literature that is constantly appearing now, but also due to the input of a wide array of contacts we have built up gradually since Volume 1, and also a slight shift towards permitting the inclusion of a little more detail than was initially envisaged. Another significant influence is the trend in global ornithology towards splitting. Although we try to steer a reasonably moderate course in the taxonomic decisions adopted in HBW, we are keen to illustrate all forms that are sometimes treated as separate species by some authors. Since 1989, things have changed considerably in this aspect, so that HBW is now more or less “obliged” to illustrate many more taxa than originally anticipated.

Returning to the business in hand, the current volume, the number of pages projected for the volume grew from a rather low original estimate steadily up towards 900+, then over 1000, latterly over 1100, and finally approaching 1200. As we already had a

number of reviewers remonstrating (with justice, we believe) that Volume 3, with its 820 or so pages, was rather heavy and cumbersome for use, especially for some of our more elderly readers, we realized that we were getting into serious difficulties.

A solution was urgently required, and we looked at all the possibilities that came to mind. The possibility of using thinner paper to reduce weight did not produce sufficiently significant results to make much difference, while at the same time it brought us to the borderline approaching transparent pages. Another obvious solution was to take up the surgeon's knife and systematically remove enough material, especially dozens (or even hundreds) of photos, to make the size more or less acceptable and manageable, but this seemed to us to amount to tearing the heart out of the book, losing masses of excellent material, wasting much that had been carefully gathered together and sorted through, and overall making the volume substantially less useful and spectacular. This option went too far against the grain with us, so we felt that some other solution was needed.

We considered converting the volume into two physical entities, Volumes 6A and 6B, but within the context of HBW this just seemed to us to be too messy and unsatisfactory, with no real advantages at all. At the same time, we were facing another major problem with the volume, that of finance. In order to cover the hugely inflated costs, arising essentially from the large number of photos to be included, but also from the increased number of plates and overall much-increased production costs – we were talking about something approaching double the number of pages, plates and photos compared with the rough average per volume so far – it became clear that the price of this outsize volume would have to be increased considerably (far more than with any previous volume) in order to meet costs, and we felt that this too would seem most unsatisfactory to many readers.

It was only after exhausting all these possibilities, and finding none of these solutions acceptable, that we finally fell back on the other obvious option, the one which seems to us much the best way out: divide the originally planned Volume 6 into two separate volumes, 6 and 7, treating each of them as an ordinary, independent volume in its own right, with the passerines now stepping back to start at what will be Volume 8. As a result of this decision, we now have the present tome, Volume 6 (Mousebirds to Hornbills), which will be followed by Volume 7 (Jacamars to Woodpeckers). Volume 7 will go ahead according to the original overall schedule, thus appearing probably some 15 months after the publication of the present volume. It would, of course, be possible to bring out Volume 7 a good deal earlier, but we feel that it would be unfair to expect the reader to pay up for two volumes over too short a period. From our own point of view, it will also give us much more time to polish up the work on Volume 7. With this decision, not only do we avoid having to exclude a lot of excellent material, we have even been able to “recover” a number of photos that we had most reluctantly felt obliged to reject for reasons of space.

We think you will readily understand that this was not an easy decision for us. Given the major implications for the rest of the series, we decided to run a poll amongst all our readers, the results of which will decide what is to be the guiding policy for the rest of the series, the passerine volumes. The aim of the poll is to find out whether our readers (a) agree with the decision we have just taken and prefer HBW to continue aiming to be as comprehensive and fully illustrated as possible, within the same general structure that is already established, probably implying an increase of three volumes in order to give the passerines the same degree of coverage; or (b) prefer to keep as close as possible to the original scheme, cutting costs where necessary, by including fewer photos and illustrating fewer subspecies on the plates, while imposing fairly strict word limits on authors. On the basis of the response to this circular the planning of the rest of the series will then be finalized definitively.

We owe everyone an apology for our failure to come to terms with reality in our original planning, and also perhaps for getting carried away by the desire to make the series as comprehensive and fully illustrated as is feasible. It originally seemed highly improbable that this could be the “problem” volume, but in the end this has proved to be the case. We apologize for any inconvenience that this might cause or have caused you personally, and can only hope that a good proportion of you will feel that we have made the right decision in putting quality before economy. Please feel free to send us any comments you may have, preferably along with your response to the circular which accompanies this volume. Thank you for bearing with us.

In addition to this, we have a few further points in connection with the present volume. All are minor, and indeed the vast majority are essentially reiterations of matters already raised in previous volumes.

In any given family, the selection of photos is planned so as to follow approximately the same sequence as the different sections of the text, starting with photos related to Systematics and ending with any appropriate for Status and Conservation. We always aim to find, wherever possible, photos that illustrate a particular feature of behaviour rather than mere portraits, while, at the same time, we give preference to those of species that are rarely (or never) seen in photos, as we believe that these will be of special interest to many of our readers, as indeed they are to us. In cases in which the family does not contain too many species, and for which there are plenty of good photos, we aim to include photos of all the species in the family. In the present volume, this is the case, for example, of Meropidae. Considerable efforts are made to get hold of the full locality details for all photos, not least because this often helps us to identify some of the less obvious subspecies. This, of course, depends on the co-operation of the agencies and the individual photographers in question, and we should like to stress that we receive a great deal of help from most agencies and all individuals alike. Nevertheless, in each volume, there are always a few photos for which the credits end up incomplete.

In the present volume we have at last managed to carry out a trial on one of our long-term aims, namely to encourage good photographers to go out in search of photos of species for which we have none of publishable quality. On this occasion, Brian Coates very kindly agreed, at very short notice and with very modest funding assistance, to travel to Sulawesi in search of photos for some elusive species. We are delighted to report that the results of this experiment include a fine series of shots, of which we are very happy to be publishing a selection in this and forthcoming volumes. It is hoped that it will be possible to continue and expand this operation in the future, and in the process to collect photos of species rarely or never before seen in photos. An extension of this same idea is to provide some form of sponsorship to encourage further research and surveys on poorly known taxa.

Since it first appeared in Volume 3, the Voice subsection in the species accounts has increasingly been felt worth including. Although originally intended only for the passerine volumes, it has proved useful in the cases of several non-passerine families too. Once the passerines are reached, this subsection will become a permanent fixture, to be supplied for all families.

The forewords to each volume aim to provide a selection of essays on various different issues that are of current interest in ornithology. In the current volume we are delighted to have been able to count on the expert participation of Don Kroodsma and the tragically departed, much loved and esteemed, Luis Baptista. As this volume has not suffered in the same way from the usual constraints of space, we encouraged the authors to speak freely and at length on their fascinating subject, avian vocalizations. We do hope that readers will enjoy this essay as much as we have.

As explained in the Introduction to Volume 5, we have continued to give the details of all restricted-range species and their presence in Endemic Bird Areas. In case anyone is uncertain, we repeat a brief definition of these two terms. As defined by BirdLife International, a "restricted-range species" is one which in historical times has had an overall range of under 50,000 km<sup>2</sup>. An Endemic Bird Area (EBA) is an area within which the nearby or overlapping ranges of two or more restricted-range species are wholly encompassed. Restricted-range species account for some 27% of the world's avifauna, or about 2600 species, and these are restricted to about 220 EBA's, which in turn support roughly 75% of all globally threatened bird species. These are thus areas of high priority for conservation, all the more so as they tend equally to be centres of endemism for other life forms.

This seems to us the appropriate moment for us to stress how delighted we are to have been able to participate in a very small way in the production of BirdLife International's important and authoritative new tome, *Threatened Birds of the World*. Also, we would like to point out that the fact that we have had early access to much of the relevant text of this latest "Red Bible" has enabled us to include major improvements for the Status and Conservation sections of many species, ensuring that they are as up to date as possible, even though the two books have actually been published merely



two months apart. Therefore, we should like to take this opportunity to extend our hearty thanks to its editors, Alison Stattersfield and David Capper, and also to the many others at BirdLife who have helped us with related matters, notably Adrian Long and Nigel Collar. We sincerely hope that we shall be able to continue our fruitful co-operation with BirdLife long into the future.

Over the years we have had a most useful interchange of ideas with James F. Clements. It is an honour for us, that he has decided to take the HBW sequence as the starting point of the fifth edition of his epic and widely used *Birds of the World: a Checklist*.

As explained in the Introduction to Volume 1, we make no particular attempt to keep fully up to date with geopolitical changes. For this reason, for the present volume we have still retained the country name Zaire, as purely for the purposes of HBW it offers certain advantages, mainly in being a more manageable name and in avoiding potential confusion. Nevertheless, it is quite likely that the decision to switch over to the current name of the country, Democratic Republic of Congo (DR Congo), may be taken for forthcoming volumes.

As ever, the accepted French, German and Spanish names come from the sources indicated in previous volumes. Missing names were again supplied by the relevant committees. Normand David and Peter Barthel once again responded most efficiently to any doubts or *lacunae* that cropped up with, respectively, French and German names. The list of recommended Spanish names continues to be published in tandem with the volumes of HBW, the last batch appearing in *Ardeola* **47**(1): 123-130.

## Acknowledgements

As ever, we are greatly indebted for the enormous amount of assistance we receive at museums. Amongst the most important for us have been the British Museum of Natural History at Tring (Robert Prys-Jones, Peter Colston, Michael Walters, Mark Adams, Cyril Walker) and the American Museum of Natural History in New York (Joel Cracraft, George Barrowclough, Mary LeCroy, Paul Sweet, Terry Chesser, Maria Rios), as well as the Louisiana State University Museum of Natural Science (Van Remsen, Steve Cardiff, Donna Dittmann, Mario Cohn-Haft, Dan Lane, Alexandre Aleixo, Jason Weckstein, Rob Faucett) and the Smithsonian Institution, National Museum of Natural History in Washington (James Dean, Gary Graves, Pam Rasmussen, Richard Zusi). We are also very grateful to the Field Museum in Chicago (David Willard, Shannon Hackett), the Kenya Natural History Museum (Leon Bennun, George Amutete, Kuria), the Colección Phelps de Venezuela (Miguel Lentino, Clemencia Rodner, Robin Restall), the Delaware Museum of Natural History (Gene Hess), the Museum of Comparative Zoology in Harvard (Alison Pirie), the National Museums of Scotland in Edinburgh (Bob McGowan), the Natuurhistorisch Museum at Leiden (René Dekker) and the Liverpool Museum (Tony Parker).

Libraries continue to provide enormous assistance in various aspects of the work. Once again, we must single out Effie Warr of the British Museum of Natural History at Tring for helping us again, and again, and again, with all manner of problems. Our grateful thanks too to the Museu de Zoologia of Barcelona (Maria Angeles Iglesias), the Sociedad Española de Ornitología in Madrid (Blas Molina) and the Estación Biológica de Doñana (José Cabot), and we also thank Raúl Aymí (Grup Català d'Anellament), Andrés Bosso and Eugenio Coconier (Asociación Ornitológica del Plata), Nicholas Gould (*International Zoo News*), Diane Seripierri (Zoology Museum, São Paulo University), Mindy Moretti (*AZA*), Marilyn Julian (*Wingspan*), Catherine Ngarachu (Nature Kenya), Brian Sykes (Oriental Bird Club), Severin Zillich (*Journal für Ornithologie*) and Steve Ramey (*Animal Behaviour*), as well as Pam Bailey, Aldo Berruti, Corinne Bos, Koen Brouwer, Thomas G. Coon, Eberhard Curio, Ellen Dierenfeld, Patricia Escalante, Mauro Fasola, M. Kinnaird, Ricardo Medina, Michele Merola-Zwartjes, D. Mudappa, T. O'Brien and Joseph M. Wunderle. Several doubts and problems arose again in connection with the scientific descriptions, and our particular thanks go to Alan Knox, but also to Murray Bruce, Normand David, Miguel Lentino and Effie Warr for their help.

Several people assisted in the form of supplying unpublished information, refereeing texts and so on. In these respects we should particularly like to thank Brian Coates, Nigel Collar, Jared M. Diamond, Guy Dutton, Geoffrey Field, Jon Fjeldså, Robert S. Kennedy, Mary LeCroy, Flávio Lima, Pete Morris, Susanne Oehlschlaeger, John P. O'Neill, Pilai Poonswad, Pam Rasmussen, Karl-Ludwig Scuchmann and Effie Warr.

We are extremely grateful to Guy Tudor once again for so generously lending us many reference photos from his sizeable collection. We have indeed been fortunate for the present volume as Robert Ridgely has very kindly checked through the maps for Neotropical species, using the huge up-to-date database amassed for Ridgely & Tudor's *Birds of South America*.

We are delighted to continue to enjoy our fruitful agreements with VIREO at the Academy of Natural Sciences in Philadelphia (Doug Wechsler), and with the National Sound Archive of the British Library (Richard Ranft). We are also very grateful to David Ascanio, Patrice Christy, Ron Johnes, Olivier Langrand, Gérard Rocamora, Clemencia Rodner, Ian Sinclair, Aurora Solé and Barry Walker, who freely provided much information to help us in the planning of some fieldwork.

Considerable efforts have been made to include the maximum information possible in the credits of each photo, and in this process agencies and individual photographers alike have been most co-operative. We should like to extend our particular thanks to Heibonsha Sachiko Kawai, who made huge efforts to get hold of the relevant details for a number of extremely "difficult" photos.

We are very grateful to Helen Horblit, who very kindly sent us the photograph of Luis Baptista for inclusion in the foreword.

The different authors and artists involved in the present volume would like to thank the Natural History Museum in Vienna (Ernst Bauernfeind, Hans-Martin Berg, Anita Gamauf), the Edward Grey Institute Library in Oxford (Linda Birch), and the Natural History Museum in Rudolstadt (Eberhard Mey), and also K. Bauer, K. D. Bishop, D. Brightsmith, C. Carter, D. Cooper, J. F. Cooper, G. Davison, Rosendo Fraga, Jörg Ganzhorn, F. González García, Steve Goodman, Frank Hawkins, H. Hoi, Jesper Hornskov, Stephan M. Hübner, Kevin Johnson, S. Keith, Meg Kemp, G. M. Kirwan, R. Liversidge, E. Lott, D. Lubman, L. R. Macaulay, G. Mackiernan, Manuel Martin-Vivaldi, Otto Pfister, M. A. Pizo, Jean Eric Rakotoarisoa, Richard Ranft, Pam Rasmussen, Thomas Schulenberg, Ian Sinclair, Russell Thorstrom, Emil Urban, P. Verbelen, David Willard, Glyn Young and Helmut Zimmermann.

Santiago Guallar kindly gave assistance with the work of revising some of the bibliographies. For help in assorted matters, our grateful thanks go to Maria Josep de Andrés, Kathleen Berge, Axel Braunlich, Dolors Buxó, Juan Antonio Cantí, Cam Christie, Mike Crosby, Dinand Derks, Fortunato Frias, Oriol Frias, Sònia Frias, Ricard Gutiérrez, Andrew Kratter, Rosa Llinàs, Isabel Martínez, Rafael Martínez, Albert Martínez-Vilalta, Paquito Montfort, María Teresa Obiols, Mary and Jim Ramsay, Olga Rius, César Ruiz and Aurea Vilalta.

Last, but by no means least, we are most grateful to Albert Earl Gilbert for very kindly allowing us to use his splendid plate for the frontispiece. This is reproduced with kind permission by Joseph Forshaw from his forthcoming book on the Trogons of the World. Yet again, we thank Toni Llobet very much for the illustration on the back cover.





# Order COLIIFORMES

## Coliiformes

Coliidae

mousebirds

Class AVES  
Order COLIIFORMES  
Family COLIIDAE (MOUSEBIRDS)



- Smallish to medium-sized arboreal birds resembling passerines, with dull grey or brown plumage, very long tail, erectile crest, and toes which can all be directed forwards.
- 29-38 cm.



- Afrotropical.
- All bushy or wooded habitats, except dense forest.
- 2 genera, 6 species, 36 taxa.
- No species threatened; none extinct since 1600.

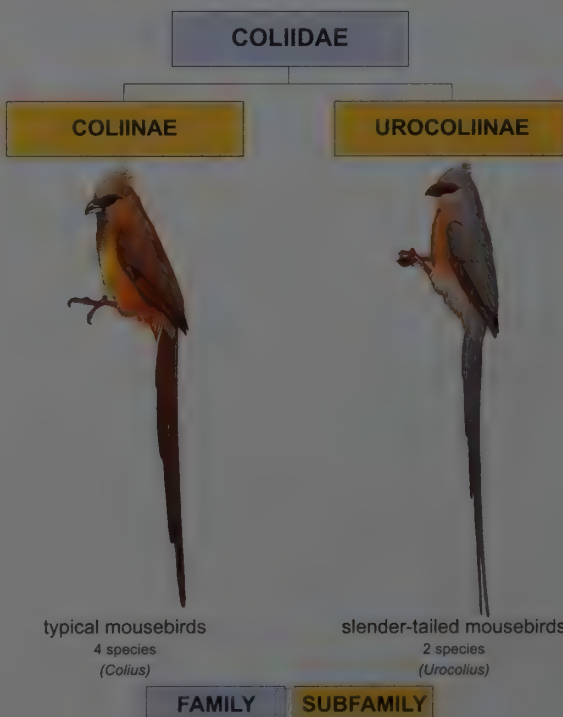
### Systematics

A tiny group of only half a dozen species, the mousebirds, often referred to alternatively as colies, possess a considerable array of very peculiar features. Given their small size and short bill, together with the short neck and short legs, they could easily be taken at first sight for very long-tailed passerines. Indeed, the very earliest classifications of birds included the mousebirds in the order Passeriformes. Their creeping movements through vegetation, often recalling those of small rodents, are responsible for their having been given the name of mousebirds. This behaviour attracts attention, as does their unusual habit of perching with the body vertically suspended between widely splayed feet, held apart at the level of the upper breast. The morphological peculiarities of the Coliidae are no less evident, comprising, for example, a desmognathous palate with very small vomers, an unusually broad pygostyle, and an ulna which is short in relation to the humerus. In addition, they have a pamprodactyl foot, an arrangement whereby all four toes may be directed forwards.

As long ago as 1872, J. Murie, after studying their osteology, proposed placing the mousebirds in a separate order. Since then, there have been several, largely unsuccessful, attempts to establish their relationship to other birds. Classifications have tended to place the Coliidae in a discrete order located among the "higher" non-passerines, wherein they exhibit various affinities with groups such as the rollers (Coraciidae), the swifts (Apodidae), the turacos (Musophagidae), the honeyguides (Indicatoridae), the parrots (Psittacidae) and the trogons (Trogonidae), among others. The DNA-DNA hybridization studies carried out by C. G. Sibley and J. E. Ahlquist not only support the group's independent status at order level, but also led those authors to propose that the mousebirds be included in a separate "Parvclass", Coliae, one of only seven comprising the Class Aves. It is quite clear, therefore, that the colies are an ancient group which, having diverged from others an extremely long time ago, have no known living close relatives.

The present distribution of the mousebirds is exclusively African. Indeed, Coliiformes is the sole order of birds that is found nowhere else but in the Afrotropical Region; furthermore, Coliidae is one of rather few avian families that are restricted to that region, others including Struthionidae, Balaenicipitidae, Scopidae and Sagittariidae, each with just a single species, and Numididae, Musophagidae and Phoeniculidae. Nevertheless, where the mousebirds are concerned, the present-day distribution seems to bear no relationship to the evolutionary origins of the group. The oldest known remains of mousebird-like birds are assigned to the

family Sandcoleidae, described by P. Houde and S. Olson in 1992 from the Lower Eocene of North America, and encompassing half a dozen genera, among them the type genus, *Sandcoleus*. Those scientists placed the Sandcoleidae in its own order, but, in view of the large number of skeletal peculiarities which it shares with the Coliidae, it seems best to include the Sandcoleidae in the Coliiformes for the time being. Members of the Sandcoleidae have subsequently been found in two places in Europe: in the London Clay of the Lower Eocene, and in deposits from the Middle Eocene of Grube Messel, in Germany. The oldest known representative of the Coliidae, *Masillacoliis brevidactylus*, was described as recently as 1998, by G. Mayr and D. S. Peters, from the oil-shales of Grube Messel. This species must have existed some 43-49 million years ago, in the Lutetian of the Middle Eocene, contemporaneously with at least one sandcoleid species of the genus *Eoglaucidium*.



Subdivision of the  
Coliidae

[Figure: Hilary Burn]

Although sandcoleids are not known to have survived beyond the Eocene, the colliids seem to have persisted for a long time in Eurasia. This is evidenced by French and German fossils assigned to the Upper Eocene of Quercy, from where the genus *Primocolius* is already quite similar to living forms, to the Oligocene of Frauenweiler, from where *Oligocolius brevitaris* was described by Mayr in the year 2000, and to the Miocene of Grive-Saint-Alban. On the other hand, the only known African fossils are relatively recent, from the Pliocene, a period which began only some five million years ago. These were found in phosphate mines at Langebaanweg, in Cape Province, and are of a species so similar to living forms that it has been included in the genus *Colius*, and named *Colius hendeyi*. The limited amount of paleontological evidence currently available may, therefore, support a hypothetical origin for the mousebirds in the northern continents, when these were extensively interconnected at the beginning of the Tertiary, and a subsequent penetration of Africa during the Miocene, when that continent and Eurasia drew together and finally met.

The six species of the Coliidae are currently placed in two genera, *Colius* and *Urocolius*, which differ substantially in skeletal and other aspects. In *Urocolius*, the bones of the wing and pectoral girdle are relatively more robust, and those of the legs and pelvic girdle relatively weaker, than those of *Colius*. This is reflected by the relative locomotory capacities of the two genera, *Urocolius* being stronger fliers and *Colius* more adept at creeping. The mandibles are relatively straight in *Colius*, but in *Urocolius* the distal half is decurved by some 20° in relation to the proximal half. *Urocolius* has a narrower tail, with five pairs of rectrices, as opposed to six pairs in *Colius*. In addition, *Urocolius* lays patterned eggs, whereas those of *Colius* are unmarked, and the pulli differ in the shape of the bill, which in *Urocolius* has a curious bulbous swelling at the base. These distinctions, among many others, have been considered by some authorities sufficient to justify the recognition not just of two genera, but of two subfamilies, Coliinae and Urocoliinae, a viewpoint supported by DNA-DNA hybridization studies. R. Verheyen proposed this division into subfamilies as long ago as 1956, but numerous subsequent authors have, nevertheless, regarded *Urocolius* as no more than a subgenus of *Colius*.

Four species are distinguishable in the genus *Colius*. The Speckled Mousebird (*Colius striatus*) is the most widespread of these, occupying much of the centre, east and south of the African continent. It completes a ring of species together with the



allopatric Red-backed Mousebird (*Colius castanotus*), which is confined to western Angola, and the White-backed Mousebird (*Colius colius*), which extends from Namibia through western and central South Africa. It is only in the latter country that the Speckled and the White-backed Mousebirds show a marginal overlap in distribution, although even there they still remain largely separated by habitat preferences. Finally, East Africa, and specifically parts of Kenya, southern Somalia and the extreme north-east of Tanzania, is inhabited by the distinctively marked White-headed Mousebird (*Colius leucocephalus*), which is



The mousebirds belong to such an ancient order that their closest living relatives are unknown. The two extant genera are outwardly very similar in appearance, but they differ in several aspects of skeletal morphology. Compared with *Urocolius*, the members of the genus *Colius* have relatively stronger bones in their legs and pelvic girdle and weaker bones in their wings and pectoral girdle. These physical differences correspond to differences in locomotory behaviour, *Colius* being more proficient at creeping through vegetation, and *Urocolius* rather stronger fliers. These Red-backed Mousebirds have the dull plumage, pronounced crest and short bill characteristic of all colliiforms.

[*Colius castanotus*. Photo: Martyn Chillmaid/Oxford Scientific Films]

The two species of *Urocolius* are allopatric, forming a superspecies that occurs throughout much of sub-Saharan Africa. The more northerly Blue-naped Mousebird inhabits a broad swath of open, semi-arid savanna and thornbush woodland from Mauritania and Senegambia in the west to Ethiopia, Somalia and Tanzania in the east. It has seven recognized subspecies, which differ subtly in coloration, eastern races tending to be darker.

[*Urocolius macrourus pulcher*, Buffalo Springs Game Reserve, Kenya. Photo: Luiz Claudio Marigo]





Although essentially an arboreal family, with legs and feet specially modified for such a lifestyle, mousebirds move about quite nimbly on the ground, in spite of the very long tail. White-backed Mousebirds occupy a wide assortment of arid and semi-arid brushy and wooded habitats from Namibia and Botswana south to the western and central portions of South Africa. They also occur in riparian woodland and have taken well to habitats created by humans, particularly orchards, gardens and thickets adjacent to irrigated agriculture.

[*Colius colius colius*, near Cape Town, South Africa.  
Photo: David Hosking/FLPA]

sympatric with the Speckled Mousebird but associated with more arid regions than those occupied by the latter species.

The two species of *Urocolius* are allopatric, and may be regarded as forming a single superspecies. The Blue-naped Mousebird (*Urocolius macrourus*) occupies a broad belt of the Sahelian and Sudanese regions, from Mauritania and Senegambia across to Ethiopia and Somalia and southwards in East Africa to Tanzania. The Red-faced Mousebird (*Urocolius indicus*) is found in the southern third of the continent, extending north to the Angolan coast, south-eastern Zaire and Tanzania.

The complexity of subspecific differentiation within the Coliidae bears some positive relationship to the geographical extent of each species' range, although it is also influenced by the degree of sedentariness of each species (see Movements) and by the degree of habitat fragmentation. Whereas the Speckled Mousebird has some twenty subspecies, well differentiated by plumage and by bill, leg and iris colours, and the Blue-naped and Red-faced Mousebirds have seven and five respectively, the White-backed and the White-headed Mousebirds each have only two subspecies, while the Red-backed Mousebird is monotypic.

H. Schifter, in his 1985 review of the Coliidae, recognized 19 subspecies of the Speckled Mousebird. He grouped these into three allopatric assemblages, which he regarded as "semi-species". The "*striatus* group", which comprises five subspecies, including the nominate, and which covers the extreme south-east of the continent from southern Malawi to the Cape, is distinguished by, among other features, an entirely black upper mandible, other races having whitish or bluish marks on the culmen. The "*leucotis* group" exhibits strikingly contrasting white ear-coverts, as the name suggests, and includes the greatest number of races, twelve in all, distributed across much of East Africa. The third and final group, the "*nigricollis* group", with only two subspecies distributed through central and western Africa, from Ghana and Angola to Zaire, exhibits the pale culmen marks, but with dull, non-contrasting ear-coverts.

## Morphological Aspects

The small body, long tail and dull brown or grey coloration are mousebird features which reinforce the group's vernacular name. The tail takes up about two-thirds of the total body length of some 30-35 cm. It is longest in the genus *Urocolius*, with the rectrices of the Blue-naped Mousebird being up to 28 cm long,

making that species' scientific name of *macrourus* clearly appropriate. Besides being long, the tail is slender and graduated, and has particularly rigid shafts. The short, rounded wings have ten primaries and ten secondaries. Other noteworthy structural attributes include a short, robust and slightly decurved bill, a usually fanned but erectile crest, short legs with relatively large toes, and strong, sharp, hooked claws. The six species are fairly similar in their measurements and masses. These are smallest in the White-headed and White-backed Mousebirds, both of which are species of arid zones and weigh some 35-40 g, and greatest in the Red-backed and Red-faced Mousebirds, weighing about 60 g.

Male and female mousebirds are alike, having a dun appearance, but the plumage generally includes some clear species-specific features. The two *Urocolius* species have a patch of bare red skin on the face and a fleshy base of the bill, while the Blue-naped Mousebird has, in addition, a conspicuous turquoise-blue nape mark. Both the White-backed and the Red-backed Mousebirds are distinguished by the markings on the rump and lower back, these being white and maroon in the former and an intense chestnut colour in the latter. The White-headed Mousebird, as the name implies, has much of the head and crest white. By contrast, the most soberly attired species, the Speckled Mousebird, has head markings which may be black, white or rufous, according to subspecies. The legs and feet of all the coliids are more or less reddish, tending towards coral-pink in *Colius* and purplish in *Urocolius*. Similarly, the adult bill colour shows generic distinctions, the ramphotheca being black and red in *Urocolius*, whereas in *Colius* it is black on the upper mandible, at least at the tip, and grey or silvery on the lower mandible.

Mousebirds are essentially frugivorous birds (see Food and Feeding). They spend most of their time in the dense foliage of trees and shrubs, through which they move rapidly and with surprising agility, continually demonstrating their acrobatic prowess. They scurry rapidly lengthwise along horizontal branch surfaces, supporting themselves with the tarsi, tail and bill. The highly flexible foot structure, which allows them to oppose one or two toes, or to turn all four forwards, makes them equivalent to species having anisodactyl, zygodactyl or pamprodactyl feet. Such feet are a special adaptation as much to their foraging style as to food-handling, being used both to help the birds gain access to food and to transfer food to the bill. The toe positions not only are continually varied, but may even differ simultaneously between the left foot and the right one. This capacity to rotate the outer and inner digits at will is made possible by a special

Mousebirds are highly social, living in groups of six to eight that occasionally swell to 20 or more birds near food concentrations. Speckled Mousebirds tend to occur in family groups. Most activities are carried out socially, the birds often very close to each other. Indeed, when roosting for the night, they huddle into a ball, hanging from a branch with their heads up and their tails pointed downwards. Clusters form each night regardless of temperature, and late-arriving individuals often try to push their way to the centre of the ball. Clustering reduces heat loss and thus results in considerable energy savings during the night.

[*Colius striatus kikuyensis*,  
Karen, near Nairobi,  
Kenya.  
Photo: Dave Richards]



arrangement of muscles and tendons which includes two small inner muscles peculiar to the group, as well as an extension to the hallux of the extensor digitorum longus, a muscle which in other bird groups, with the exception of the cockatoos and parrots (Psittaciformes), inserts solely on the anterior digits.

The unusually forward-placed and laterally displaced legs of the mousebirds perhaps enable them to rotate these limbs more widely and effectively. Nevertheless, their adaptations to arboreal creeping do not seem to inhibit their ability to move on the ground, where mousebirds show themselves to be reasonably nimble in walking, running or jumping, which they do generally with the hallux and the fourth toe directed backwards.

Very probably, the strange perching style of mousebirds is related to the forward position of the legs themselves. Although mousebirds can perch briefly in the same manner as that of other birds, their usual habit is to hang with the belly down between the legs and with the feet at upper-breast level. In this position, they generally use the tail or lower abdomen to prop themselves against some support, frequently a small branch but also very often the body of some neighbouring flock-member. When thus suspended, they are able to engage an anatomical device, such as that possessed by bats, which permits them to hang without additional energy expenditure, a feature which explains instances of dead birds having been found still perched. The flexor tendons of the toes pass through a grooved sheath, which is also present in other birds and which serves to restrain slippage, but which is particularly effective in the Coliidae, given that these have particularly thick tendons enclosed by a striated epithelium. It is also the case that these tendons do not insert at the bases of the outer phalanges but, instead, do so more distally so that, when the leg is flexed, the claws automatically move downwards.

Mousebird flocks typically move in line from bush to bush and by means of short flights in which glides are alternated with brief bursts of vigorous flapping. The body and tail shapes and the flight styles of these birds have prompted comparison with parakeets or miniature pheasants (Phasianidae), or even with "arrows flying feathers-foremost". They generally descend from the apex of a shrub to the base or middle portion of another, in which they land rather boisterously. The short, rounded wings, typical of species which inhabit dense cover, allow considerable bursts of speed, the Red-faced Mousebird having been timed at 74 km/h, but they probably do not permit particularly lengthy or sustained flights.

The plumage of mousebirds also displays some peculiar features. The contour feathers cover the body almost uniformly, leav-

ing only one or two apteria on the head. There is no down, but on the other hand the aftershafts are unusually long, each one being up to four-fifths the length of the main shaft. In addition, the contour feathers have loose distal barbs owing to the incomplete development of the barbules, which may be an interesting adaptation to moving unobtrusively through dense scrub, and which confers a soft, hair-like and, indeed, mouse-like quality to the plumage.

As with so many other tropical bird species, the moult occurs throughout the year and is apparently not influenced by the demands of reproduction or migration. Reproduction is not particularly demanding energetically, given the small clutch sizes (see Breeding), while migration is virtually non-existent (see Movements). A seasonal pattern of primary moult has been reported only from South Africa, where the climate is more temperate. In that region, primary moult was apparent in 80% of individuals of the Speckled and the Red-faced Mousebirds examined between November and April, in contrast to only 25% of the Speckled and no Red-faced at any other times of the year. Also in South Africa, there is a tendency for nesting to be concentrated between August and October, so that the main moult period becomes post-nuptial, as is generally the case among species living in temperate and cold countries.

Plumage replacement by coliids is so slow that some individuals, such as those of the Speckled Mousebird in Tanzania, have been described as being in a nearly permanent state of moult, or even as having an overlap between two successive moult cycles. The moult patterns, too, are very irregular. Although replacement of the flight-feathers seems to follow the pattern most commonly seen in birds, with the primaries replaced descendantly and the moult of the secondaries beginning at both extremities, the mousebirds exhibit irregularities and exceptions of all kinds. The lack of any regular moult sequence is the norm where the rectrices are concerned, where the longest feathers are subject to much abrasion and may even show worn tips before they are fully grown.

## Habitat

Mousebirds of one or another species can be encountered in an extremely broad range of Afrotropical habitats, avoiding only dense forest, extreme desert regions and mountain peaks. In effect, these birds occupy virtually any type of scrub or light woodland, from semi-desert to forest edge and second-growth forest. In addition,



they adapt readily to habitats modified by human activity, being frequent or abundant in cultivated land, in areas colonized by exotic flora, and also in suburban or urban parks and gardens. All this apart, interspecific differences in habitat selection exist which are often related to climatic factors, and which become most apparent where the ranges of different species overlap.

Most of sub-Saharan Africa is covered by the combined geographical ranges of the members of this family. Nevertheless, there are at least three extensive regions from which the mousebirds seem to be totally absent. One of these is the great expanse of lowland evergreen forest in the Congo Basin. A second region, their absence from which is hard to explain, extends across the countries to the north of the Gulf of Guinea, from southern Senegambia to eastern Nigeria, within which colliids have been reported only from a small part of Ghana, the Mole Game Park, which has an isolated population of Speckled Mousebirds. The third region covers most of eastern and central Angola, a region dominated by *Brachystegia* woodland; this is also a habitat which mousebirds avoid, perhaps because of a lack of adequate food during the dry season. At the other extreme, three species overlap in just two areas, both of limited extent, one around Kenya and the other in the centre and south of southern Africa. Hence, it is not possible to find more than one or two species at a time over most parts of the Afrotropical Region. Even where three species occur, they tend to be segregated by habitat and are unlikely to be seen together in a single locality.

The species which is most often found with other members of the family is the Speckled Mousebird, the most widespread of the Coliidae and one which seems to favour more mesic or even humid climatic regimes. Where such overlaps involve only one other species, the latter is generally of the genus *Urocolius*, the Blue-naped Mousebird in the north and the Red-faced Mousebird in the south. Both *Urocolius* species appear to tolerate a wide range of climatic conditions and, given their superior flying ability, they may exploit the habitat in different ways. Where three species co-occur, they include a second *Colius* species with an affinity for arid zones, this being the White-headed Mousebird in East Africa and the White-backed Mousebird in southern Africa. There seems to be a greater overlap in habitat between the Blue-naped and the White-headed

Mousebirds in Kenya, but the latter's range there is fragmented and its population densities are low.

In southern Africa, the three species which may share similar habitats nevertheless display a considerable degree of flexibility in habitat selection, although with one or other species being numerically dominant in any given region. Here, the White-backed Mousebird is most abundant in the west; tolerating very arid conditions, it flourishes in the Karoo and the Kalahari and it penetrates the Namib Desert. In contrast, to the south and east, the Red-faced Mousebird seems to thrive best in various types of thorn-woodland, and the Speckled Mousebird in denser vegetation such as euphorbiaceous bush or macchia, where it may find a more humid micro-climate.

In mountain regions, the Speckled Mousebird has been reported at an altitude of 1800 m in Zimbabwe, at 2300 m in Cameroon and above 2500 m in Kenya. Nevertheless, in the southern highveld of, for example, Lesotho, it soon becomes rare or absent, its limits being marked by the  $-7^{\circ}\text{C}$  isotherm, corresponding to the average minimum temperature of the coldest month, July. Other species are more restricted to lower altitudes: in Kenya, for instance, the Blue-naped Mousebird does not normally range above 1600 m, nor the White-headed Mousebird above 1400 m. In arid lowland regions, on the other hand, even the most tolerant species tend to seek out the most vegetated zones, such as those along watercourses or, very frequently, in irrigated farmland.

### General Habits

Mousebirds occur in flocks throughout the year, even when breeding. These are usually small groups, of about half a dozen individuals, but larger gatherings of 20-30 or more birds occur where food is abundant, or at roosts. Isolated pairs or individuals are only occasionally encountered. For the Speckled Mousebird, studies carried out in Gabon, Congo and Cameroon have revealed mean flock sizes of, respectively, 7.0, 8.4 and 8.5 birds. These tend to be family groups, comprising both adults and immature birds, apparently centred on related males. The groups show notably strong social cohesiveness. All daily activities, including

Living in such tight-knit groups, and with such a proclivity for physical contact, mousebirds have well-developed social behaviour. Allopreening, as demonstrated by these Red-faced Mousebirds, is extremely common. It is often directed at body parts that are difficult for a bird to reach on its own, and the birds often reciprocate in each preening the other. In addition, allopreening may be a form of ritualistic behaviour that functions to reduce aggression and maintain the group cohesion that is so characteristic of mousebirds.

[*Urocolius indicus transvaalensis*, Johannesburg, South Africa.  
Photo: Brendan Ryan/Planet Earth]





The gregariousness that is so typical of colies is clearly demonstrated by this assembly of dust-bathing Speckled Mousebirds. Members of this family devote a substantial part of their day to plumage upkeep and to resting. Groups frequently dust-bathe, sometimes with one individual abstaining in order to keep an eye open for predators. Dust-bathing, like sunning, probably serves to decrease ectoparasite loads and also to aid in feather maintenance.

[*Colius striatus kikuyensis*,  
Karen, near Nairobi,  
Kenya.  
Photo: Dave Richards]



foraging, resting and grooming, are carried out communally, with constant vocal communication being maintained. In addition, flock-members very often make direct physical contact with one another, without showing the respect for individual distance demonstrated by other gregarious bird species. Perched mousebirds often prop themselves against each other, belly to belly. Furthermore, at various times during the day, and invariably when roosting, all members of the flock huddle closely together. Allopreening is seen much more frequently than it is among other avian species, and it has an obvious social function, together with food-offering, perhaps reflecting group hierarchies.

This mutual attraction between conspecifics seems to allow mousebirds to accept newcomers into their flocks relatively willingly. M. K. Rowan, who studied these birds in South Africa over many years, relates how wild mousebirds used to visit captives in her outdoor aviaries, attracted by their calls, and how they would perch on the cages and even preen the inmates. Similar observations have often been made elsewhere. There is even an instance of captive Speckled Mousebirds passing food to wild visitors. Despite such behaviour, however, and in contrast, violent territorial conflicts between flocks of that same species have been reported, both in Gabon and in Congo, as well as instances where captive groups have killed individuals which have been newly added to the cage.

Feeding activity, which occurs at widely spaced intervals throughout the daylight hours, seems to take up a relatively small proportion of the daily routine of mousebirds (see Food and Feeding). Much more time is devoted to resting and to plumage maintenance. The latter involves frequent dust-bathing on the ground, water-bathing or the use of dew being relatively rare. Such baths may help to reduce ectoparasite loads, which seem to be high in mousebirds, probably as a result of their propensity for frequent shared body contact. Observations on captives held in aviaries suggest that dust-bathing groups always post a sentry, a duty which is rotated among flock-members. Sun-bathing is frequent, too, especially in the early morning, when it may serve to dry the plumage, and just before sunset.

Groups rest regularly, and their members then often form clusters, especially during cold or wet weather. For Speckled Mousebirds in Congo, S. Yamagishi and G. Kabango recorded such behaviour twelve times a day on average, for up to 39 minutes at a time, the mean duration of rest periods being 7.6 minutes. It is not surprising, therefore, that these birds tend to cover little ground each day: groups of Speckled Mousebirds may travel less than 500 m per day, and their average home ranges have been reported as only 3.3 ha in Congo and 3.5 ha in Gabon. The Gabon

study additionally revealed that there is a core territory of less than 1 ha where roosts and nests are located, and that the birds may range annually over an area of between 10 ha and 15 ha.

Sleeping mousebirds form clusters in trees or shrubs, accommodating between half a dozen and a dozen individuals, sometimes more, irrespective of whether the weather is warm or cold. Captive mousebirds do the same. Clustered individuals hang in their customary posture, not head-down as in the manner of bats or hanging-parrots (*Loriculus*) as was long thought to be the case, although this erroneous belief is still sometimes repeated in print. They sleep with the head hunched between the shoulders, as if to minimize the body surface area. Cluster formation seems to involve competition for the innermost places, late arrivals often trying to push in. Mousebirds spend relatively more time sleeping than do other birds, gathering at roosts before sunset and not leaving until 15 minutes or half an hour after sunrise, even on fine days. As a result, they sleep for over twelve hours a day in equatorial latitudes, and for around 14 hours a day during the winter months in South Africa.

The rather indolent behaviour of mousebirds, coupled with their frequent sun-bathing and their habit of clustering together when resting or sleeping, suggested to earlier ornithologists that these birds' thermoregulatory strategies might be unusual, or even that the Coliidae might be "imperfectly endothermic". Without going that far, it is certainly the case that in this respect, too, the mousebirds are quite original. Various authors, from A. Brehm in the early twentieth century onwards, reported observations of captive individuals which showed that the mousebirds can enter into torpidity. Thus, in the 1950's, R. B. Cowles, after noting how a Speckled Mousebird that was kept in the dark exhibited significant falls in body temperature, from 38°C to 24°C, wrote that these birds "can and do experience cold torpor probably as a fairly regular and normal physiological phenomenon". This possibility was over a long period regarded with a certain scepticism, not least because mousebirds did not appear to be particularly cold-sensitive and could withstand low nocturnal temperatures without displaying any signs of lethargy. In addition, cases of extreme hypothermia were reported in which birds had been accidentally soaked through by heavy downpours of rain and the affected individuals had quite often died. In 1970, G. A. Bartholomew and C. H. Trost finally succeeded in inducing torpor in captive Speckled Mousebirds, not by altering the ambient temperature or humidity, but by limiting the birds' food intake until the body mass of each was reduced by between 10% and 15%. The underweight birds entered a state of lethargy each night, during which their temperature fell to less than half the normal level and their oxygen consumption was much

diminished, indicating reduced metabolic activity. The birds were able to raise their body temperature to normal unaided, in gradual stages, shortly before first light. It was apparent, therefore, that they possessed physiological mechanisms enabling them to save energy at night.

This interesting process has been studied in depth by R. Prinzinger and his collaborators, lately using transmitting sensors implanted in the peritoneal cavity which allow body temperature and other interesting parameters, such as heart rate, to be monitored continuously. These studies have revealed, among other findings, that nocturnal torpor occurs in at least four species of mousebird, and that it is invariably associated with a decline in body mass below a certain minimum. Those individuals which have access to unlimited food and have a normal body mass show a modest regular drop in body temperature at night, from approximately 42°C to 40°C in the Blue-naped Mousebird, and reductions in heart rate by about 20% and in metabolic rate from 120-140 J/g-h to around 80 J/g-h, following a circadian cycle comparable to that of many other endotherms, both mammals and birds. In contrast, those subjected to a restricted diet show an exaggerated response: their body temperature falls to 20-25°C, the heart rate declines from 250-300 to some 200 beats a minute and the stroke volume to less than half the normal, with the metabolic rate falling to scarcely 20 J/g-h. By these means, the mousebirds undoubtedly achieve significant energy savings, of the order of 90% when torpid and some 30% over a whole day.

Such strategies do, however, have their costs. Torpid birds are practically incapable of normal reactions, and so they may fall easy prey to nocturnal predators. In addition, if they are caught unawares by a rainstorm and become thoroughly drenched, with consequent loss or severe impairment of the insulating properties of the plumage, then they are at risk of irreversible hypothermia, bearing in mind that spontaneous arousal seems to be no longer possible once the body temperature falls below 18°C. Because the mousebirds lack down and the distal portions of their contour feathers have loose barbs (see Morphological Aspects), they would appear especially prone to such drenching. As a result, instances in which mousebirds are found dead on their perches, "drowned" by downpours, are relatively frequent. This risk further explains the clustering behaviour described above, as well as the tendency for roosts to be in sites affording particular shelter from rain.

It may seem surprising that torpor should be displayed by birds which are not particularly tiny, as are the hummingbirds (Trochilidae), nor dependent upon such a fluctuating and seasonally variable food as aerial insects, as is the case with the swifts or the nightjars (Caprimulgidae). The explanation may, nonetheless, revolve around dietary considerations, the basically frugivorous diet of the Coliidae being of very low calorific value and food itself being subject to periods of shortage in certain geographical areas (see Food and Feeding). Several other aspects of mousebird behaviour accord well with the consequences of energy shortage that results from the specialized diet of these birds. These include the frequency of sun-bathing and the habit of clustering. Laboratory studies have shown that the latter enables significant energy savings: individuals of the Speckled Mousebird grouped in clusters of four birds show basal metabolic rates about 20-30% lower, depending on the ambient temperature, than those of isolated birds. The employment of solar energy must also be important, given the high frequency of sun-bathing and also the manner in which it is performed: the birds expose the ventral surface, wings opened in an arc, in which posture the sparse plumage and the heavily pigmented skin no doubt assist in the absorption of solar radiation.

## Voice

The complex social organization of the mousebirds, and perhaps also the fact that they live in dense habitats where visibility is often restricted, may together explain their possession of a considerably rich repertoire of vocalizations. For some species, field observations have been supplemented by aviary-based studies, which have detected low-intensity calls that are sometimes un-

noticed in the field. These studies of captives have also made it possible to relate specific calls to particular aspects of behaviour with a greater precision. In this manner, a repertoire of 21 calls has been revealed for the Blue-naped Mousebird. Of these, five are related to group cohesion, two concern cluster formation, five involve various aspects of agonistic behaviour, three are associated with courtship, one is linked with incubation, and the remaining five occur during the earliest stages of the mousebird's life; two of these last occur within the egg, and three are specific to nestlings or juveniles.

Mousebird flocks maintain vocal contact continuously, with muted chattering when the birds are in close proximity. When perched atop a tree or shrub and about to take flight, or when flying from one spot to another, they use characteristic high-pitched contact calls. In the latter context, the two genera differ substantially. Whereas in *Colius* these calls are short and have a harsh or buzzy quality, for example "chew-chew" in the Speckled Mousebird or "tsik-tsik-tsik" in the White-headed Mousebird, the two *Urocolius* species emit long, clear and melodious whistles, often far-reaching. Those of the Red-faced Mousebird have been transcribed as "tree-ree-ree" or "ti-wi-wi-wi", and those of the Blue-naped as "peeee, peeeeeeeee", such whistles being accompanied by obvious throat movements. The contrast in call types between the two genera has been said to be due to their different mandible structures, the lower mandible being straight in *Colius* and angled in *Urocolius*, as described above (see Systematics). It may also be related to differences in flying ability between the two, the superior flying powers and consequent wider-ranging behaviour of *Urocolius* requiring more powerful contact calls in that genus. It is certainly the case that adults of the Blue-naped Mousebird have two types of contact call, one for short-distance and the other for long-distance communication.

Various alarm calls are uttered on the approach of potential predators. In the case of the Speckled Mousebird, at least, a distinction seems to be made between terrestrial threats, when the call is a strident "shriek", and flying raptors, when an explosive "pit" is used. Alarm calls vary in intensity, and very often are uttered in quick succession, during which the bird's crest is alternately raised and lowered.

Crest movements and those of the bill and other parts of the body, along with vocalizations, are frequently involved in other contexts, together comprising an extensive repertoire of ritualized signals. Similarly, ritual presentation of fruit or leaves is often observed.

## Food and Feeding

Mousebirds feed mainly on fruit, in various states of ripeness, but they also take other plant material such as leaves, shoots, buds, flowers and nectar. In South Africa, Rowan studied the stomach contents of a total of 63 individuals of three coliid species, collected throughout the year in different areas. She found that, apart from a few birds with empty stomachs, 50% had eaten fruits alone, 30% a mixture of fruits and leaves, and 20% only leaves, these proportions being similar for all three species. Observations on Speckled Mousebirds in Gabon show that leaves are eaten more often in the afternoons, a leaf "supper" preceding sunset. Nevertheless, the diet of captive mousebirds consists almost entirely of fruit.

The range of plant species exploited is very broad. For example, and considering fruit consumption alone, no fewer than 40 species have been recorded as being taken by the Speckled Mousebird in South Africa, with 27 fruit species consumed in Cameroon and 22 in Gabon. Nevertheless, there are very often specific plants which, because of their local abundance, or for some other reason, seem to be especially appreciated by one mousebird species or another. The Blue-naped Mousebird, for instance, appears to depend on *Salvadora persica* in various parts of the Sahel, this plant also being very important to Red-faced and White-backed Mousebirds in the Namib Desert. Similarly, Speckled Mousebirds in Gabon depend chiefly on *Solanum torvum*. Plant genera which are cited as particularly important in the diet of mousebirds in-



These Speckled Mousebirds have adopted the stereotyped posture of a sunning colliiform, with their undersides tilted towards the sun, their body feathers erected to expose the skin, and their wings opened in an arc at either side of the body.

Sun-bathing is a very common practice in mousebirds and probably serves a variety of functions. For example, it may discourage the high loads of ectoparasites that can build up in mousebirds because they so often come in close contact with each other. Sunning also may dry the plumage, and perhaps more importantly, it may aid in thermoregulation. Mousebirds periodically become limited in terms of energy because they specialize on fruits that are low in calories and that are sometimes in short supply.

Accordingly, mousebirds have evolved the ability to go into torpor during periods of energy shortage. Torpid mousebirds reduce their normal body temperature of 42°C to 20-25°C, resulting in substantial energy savings.

Maintaining normal body temperature via sun-bathing is probably very important to these birds during daylight hours.

Moreover, mousebirds have heavily pigmented skin, which no doubt enhances the absorption of solar radiation when the birds expose their skin to sunlight.

[*Colius striatus minor*, Nylsvley, South Africa. Photo: Warwick Tarboton]





clude *Lycium*, *Solanum*, *Ficus*, *Rhus*, *Phoenix*, *Balanites*, *Tamarindus* and *Diospyros*, among many others.

The above details apply to native plant species, but nowadays there are large areas where mousebirds rely more and more on exotics. These include those introduced as human food, such as mangoes, pawpaws (papayas), peaches, tomatoes, figs, strawberries, grapes, peas and almond flowers, or as ornamentals, including *Jacaranda*, *Azadirachta*, *Cotoneaster* and others. Even non-native weeds can be important foods of these birds, as is the case in South Africa with the American *Opuntia*, the European *Rubus* or the Australian *Acacia cyclops*.

All coliid species seem to have similar diets. Of a long list of food types taken in South Africa, for example, 80% were shared by at least two species and 30% by all three mousebirds present.

A surprising feature of mousebird diets is that they include, in good measure, many plants which are toxic to other animals. Among these, Rowan records for South Africa the syringa (*Melia azederach*), the pepper tree (*Schinus molle*), the bugweed (*Solanum auriculatum*) and even, as an extreme example, the bushman's poison (*Acokanthera spectabilis*), used by bushmen and other peoples for preparing poison-arrows.

Given the wide range of plants used by mousebirds, and the birds' lack of strict dependence on fruits alone, food availability might be thought to be fairly uniform throughout the year. This does, indeed, appear to be the case in South Africa's Cape Province, with its Mediterranean climate, where fruiting native plants are always available and where even arid years seem to pose no dietary problems for mousebirds. Farther north, however, in Gabon, a detailed study by J. P. Decoux showed that the fruiting period of berry-bearing shrubs is very irregular there, and that this, together with the effects of slash-and-burn farming, leads to substantial local variation in food availability for the Speckled Mousebird.

Mousebirds have a short, wide gut, lacking caeca, as might be expected of frugivores, and food transit through this is very rapid. In the Blue-naped Mousebird, the intestine of which averages 19 cm in length, the faeces are voided between 6 and 18 minutes after ingestion of fruits. The transit is much slower when leaves are consumed, which may explain why leaves are often chosen as the final meal of the day. Stomach contents have been found to average 2.5 g in weight for South African species. All this results in feeding bouts being brief and regularly spaced throughout the day. In captivity, and with food available *ad libitum*, mousebirds visit the feeders at a rate of about three times an hour and consume around 5 g of fruit in that time; over a whole day, this amounts to a substantial intake of food, the equivalent of the individual bird's body weight. Each meal is very rapid, its consumption taking barely half a minute in aviary studies. Digestive efficiency is low, measured at 71% in the Blue-naped Mousebird in laboratory studies, although this compares favourably with other frugivores, where the usual range is between 30% and 70%. Sugars are, in the main, metabolized, cellulose being egested.

Food of animal origin is noted from time to time in the coliid diet. There are numerous records of mousebirds capturing insects such as winged termites, as well as what seems to be an exceptional observation of several Speckled Mousebirds at Mountain Lodge, on Mount Kenya, which were attracted to both raw and cooked meat put out to entice carnivorous mammals. Mousebirds have also been accused of taking the nestlings of other birds on occasions. Furthermore, it has been pointed out that the high levels of infestation with tapeworms (Cyclophyllidae) which mousebirds sometimes exhibit are difficult to explain in the absence of an animal component in the diet, although it has been suggested that the birds may become infested by taking foods contaminated by the faeces of other individuals of their own or another species. Certainly, captive mousebirds appear to show no interest in meat, mealworms or other material of animal origin, apart from ant pupae which they sometimes feed to their young.

It may be that the animal component in the diet is very rare, and that it corresponds with very specific and transient nutritional requirements. This may apply also to observations of mousebirds eating earth, such as those made by J. P. Chapin in Zaïre. There, groups of Speckled Mousebirds were seen regularly to visit a particular cave, where they filled their stomachs

with a red lateritic soil of significant salt content. Similarly, in Gabon, Decoux observed the tendency by the same species to take clay-rich soil at the time of the evening leaf meals, as was evident from faecal deposits below roosts.

Under normal conditions, the high water content of the diet makes drinking unnecessary, but this activity has been observed in various colliids. Both White-backed and Red-faced Mousebirds have been seen at water-holes in the Namib Desert, although only during periods when supplies of ripe *Salvadora* berries have been exhausted and when only small, underdeveloped, bitter ones are available. Speckled Mousebirds in Gabon often take drops of dew or rain from leaves. It is possible that the various species may differ in their need for water. As an example, the Speckled Mousebird seems to require water more than does the White-backed Mousebird, this being reflected in the latter's tendency to frequent more arid habitats and to produce much drier, more powdery faeces than those of the former species.

When they do drink, the mousebirds reveal a further peculiarity. They do not raise the head to swallow each mouthful, but are able to suck up water in the manner of pigeons (Columbidae).

## Breeding

The gregariousness of mousebirds is maintained during the breeding period, when nests are frequently found close together in loose colonies which, at least on some occasions, are clearly associated with high local availability of fruit. Nevertheless, nests are more widely dispersed in many cases. Pairs are essentially monogamous and long-lasting, although there are exceptions. It is also frequently the case, although not invariably so, that mousebird pairs rely on helpers when nest-building, incubating and caring for the young, both within the nest and subsequently. Precise data on this latter phenomenon are lacking for most species, but the intensive study of the Speckled Mousebird in Gabon, carried out by Decoux, revealed the regular presence of between one and three male helpers, usually offspring of the breeding pair, as well as a similar number of satellite females. These females appear from elsewhere, and they occasionally lay eggs in the nest of the principal pair, this having been recorded in 2% of cases. Rowan also gives evidence of communal or co-operative breeding of mousebirds in southern Africa, where up to a third of nests may hold eggs of two or more females.

Although breeding attempts take place throughout the year, peak periods occur. These differ between regions and are more or less related to cycles of food availability. In the case of the Speckled Mousebird in Gabon, clutches are laid in all months but are most frequent towards the end of each of the two dry seasons, thus coinciding with the periods of maximum availability of the fruits of *Solanum torvum*, the principal food item there. On the other hand, in the south-east of Cape Province, in South Africa, 70% of breeding attempts by this same species fall within just three months, August, September and October, when rising temperatures following the winter rains lead to a rapid growth of vegetation. In areas where rainfall and food supply are unpredictable, the ability to nest at any time of the year may be regarded as a useful adaptation, as seems to be the case with the White-backed Mousebird in the arid regions of the Karoo and Namibia.

The complex social life of these birds must provide many opportunities for synchronizing the reproductive cycle of pairs. Mousebirds have no songs as such, but they do have various calls which may be attributed to courtship, as well as associated behaviour such as allopreening and courtship feeding. In addition, there is a peculiar pre-copulatory display, first reported for the Red-faced Mousebird and subsequently for the other species, with the exceptions of the little-studied Red-backed and White-headed Mousebirds. In this display, known as "jumping" or "bouncing", an individual sits erect on a solid branch, or even on the ground, and moves rhythmically up and down for some minutes without leaving its perch or, more often, leaps up to four centimetres in the air. The display involves both males and females, as evidenced by their final roles, and terminates when one individual approaches the other and copulation occurs, accompanied by billing and allopreening.



While drinking, mousebirds suck water into the mouth and then swallow it without raising the head, an unusual ability that they share with pigeons (Columbidae).

The amazing agility of mousebirds is illustrated in their ability to hang upside-down, as demonstrated by this Red-faced Mousebird.

This agility stems from certain physical features of the family. Mousebirds have short legs that are positioned well forward on the body and are displaced laterally, allowing the birds to perch in an unusual fashion and to move around acrobatically. Perched mousebirds typically hang with the belly lowered and the legs splayed out to the sides so that the toes are held at breast level. A special arrangement of the muscles and tendons in the feet allows the first and fourth toes to be rotated forwards or backwards so that the position of the toes may be anisodactyl, zygodactyl or even pamprodactyl, with all four toes pointed forwards; indeed, the toe position may differ from one foot to the other simultaneously!

[*Urocolius indicus*  
*transvaalensis*,  
north-west Cape Province,  
South Africa.

Photos: HPH Photography/  
Bruce Coleman]



Mousebirds build their nests in trees and bushes. The nests themselves are similar to those of many passerines: an open-bowl structure with a basal platform and fine lining. Both sexes take part in nest construction, in some species the males bringing the materials and the females doing the actual building. The nest platform of the two species of *Urocolius* consists of dry, branched and often thorny twigs, but at least two of the four *Colius* species, the Speckled and the White-backed Mousebirds, more often include green stems and other relatively flexible plant material in this structure. Occasionally, old mousebird nests, or those of other birds, are dismantled to enable new ones to be constructed. The nest lining can include a surprising variety of materials: grasses, leaves, mosses, lichens, hair, wool, cotton wool, cobwebs and, near towns or villages, bits of cloth, paper or string. In addition, various species decorate the nest externally with flowering sprays, and furthermore, for unknown reasons, green leaves are added to the lining once eggs or chicks are present. The external decoration may serve to camouflage the nest, which is generally well hidden in the foliage, the leaves of creeping plants sometimes being made use of to aid concealment.

Other forms of nest protection include the selection of sites that are difficult of access, or in positions at some height from the ground. Nest-sites within thorny trees or shrubs are preferred by southern African species. Others elsewhere are located near wasp nests, as with Speckled and Red-faced Mousebirds in Namibia which chose to build near nests of the aggressive wasp *Belanogaster rufipennis*. Mousebird nests have been found from 1 m to 7 m above the ground, although a range of 2-3 m seems most usual. In southern Africa, nest heights are determined partly by the height of vegetation in particular zones and also by species-specific preferences, the Red-faced Mousebird selecting the highest sites. It has been demonstrated that rates of nest predation are, as might be expected, inversely proportional to nest height. Thus, the Red-faced Mousebird loses about one-third of nests built at a height of 2.5 m or less, one-fifth of those situated between 2.7 m and 3.7 m and only one-sixth of those placed at about 5 m or more above ground. The question arises as to why the Speckled Mousebird, which suffers significantly more nest losses than does the Red-faced Mousebird, should regularly locate its nests at lower heights. Perhaps energetics are involved, the former species being a weaker flier. The use of thorny shrubs also seems to be an effective strategy: a study of Speckled Mousebirds in Gabon found that 70% of nests in such sites were

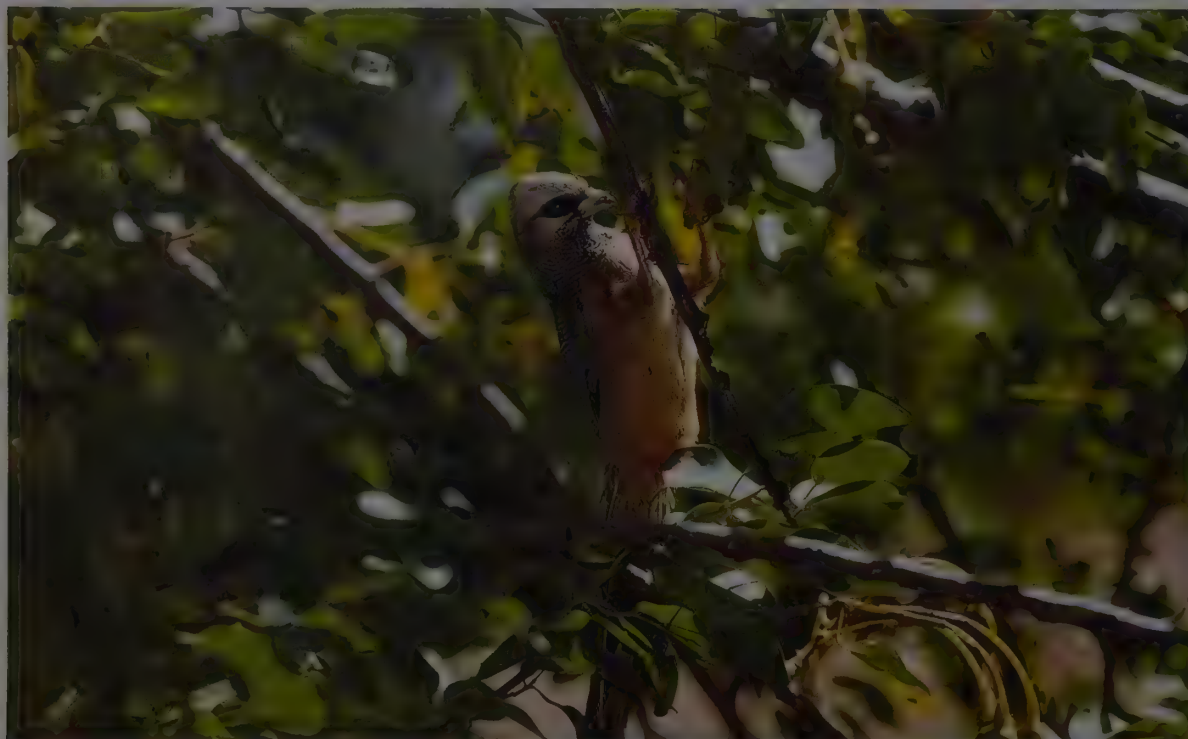
successful, as opposed to an average success rate for all sites combined of 44%.

The eggs, which are oval in shape, noticeably rough-textured and whitish, with some brownish-red markings in *Urocolius* but unmarked in *Colius*, are surprisingly small. They average 21-22 mm long and 16-17 mm wide, and weigh less than 3 g. This is only 5% or less of the female mousebird's weight, a situation paralleled in the avian world only by the parasitic cuckoos (Cuculidae). Clutch sizes are small, generally two or three eggs, provided that only one female is involved, which, as already mentioned, is not always the case. The eggs are laid at intervals of at least 24 hours. Incubation starts with the first egg and involves both parents, and sometimes helpers as well. It is not unusual to see two birds incubating at once, or several sleeping together on the nest at night. In the Speckled Mousebird, the incubating bird is relieved frequently, every 45 minutes on average, this undoubtedly being related to the customary feeding pattern (see General Habits, Food and Feeding). The change-over is accompanied by ritual gaping and tongue-showing or by presentation of a leaf by the male. Incubation periods are very brief, around 12 days.

On hatching, the altricial young weigh 2 g or less, are blind and, especially in *Urocolius*, are covered with a sparse down which leaves the head, neck and much of the back bare. Chicks of the Speckled and White-backed Mousebirds, and possibly of the two other *Colius* species, have a brilliant yellow tongue which contrasts with the gape. Nestlings of the two *Urocolius* species have curious bulbous swellings at the base and on both sides of the lower mandible, giving them a strange frog-like appearance when they beg for food. The young are brooded continuously, even when they are already well feathered, and with considerable tenacity, as is also the case with incubation of the eggs. Indeed, the sitting adult sometimes has to be forcibly lifted off the nest in order to inspect its contents.

The mousebird nestlings are fed by regurgitation. Their faeces, which are soft and not encapsulated in sacs, are swallowed by the parents. This behaviour serves to maintain nest hygiene and may also be a way of maximizing food resources, being perhaps a form of refection comparable to that of such animals as lagomorphs and koalas (*Phascolarctos*). In fact, the Speckled Mousebird in Gabon usually feeds its chicks on a mixture of fresh material and droppings.

Fledging periods of the Coliidae are brief, lasting some two and a half weeks. Sometimes they are even shorter, given that,



Hanging vertically with its feet at head level, this White-headed Mousebird is feeding on the contents of an unripe pod. Little is known about the diet of this species, but it is likely that it is mostly made up of fruit. Indeed, all mousebirds are largely frugivorous, although they also eat leaves, flowers, buds and nectar from time to time. Mousebirds have a short gut, and the fruits they consume are passed through the digestive tract rather quickly. Feeding bouts are brief, however, and are regularly separated with periods of non-feeding activity during the course of the day.

[*Colius leucocephalus turneri*, Buffalo Springs Game Reserve, Kenya. Photo: Rob & Ann Simpson]



The Speckled Mousebird has been recorded eating raw and cooked meat that was set out to attract carnivorous mammals, but studies in South Africa, Gabon and Cameroon have firmly established that, as in the case of other mousebird species, fruits and flowers of various species of plant make up the bulk of its diet. Indeed, in some areas it consumes cultivated fruits, vegetables and ornamental plants, with the result that it is branded an agricultural pest.

[*Colius striatus kikuyensis*, Lake Baringo, Kenya. Photo: Alan Hartley/Oxford Scientific Films]



after ten days, the young are capable of creeping out of the nest, which they may do at times; indeed, they may even leave the nest permanently at this age if they feel seriously threatened by a predator. Beforehand, the first quills appear at around four days of age, and the eyes open on the sixth day, when the first vanes of the remiges begin to emerge from their sheaths. Under normal circumstances, the young fledge at scarcely half the weight of the adults, with a very short tail but with almost full-size wings, which allow them to take short flights. They have a very short crest and a peculiar triangular bald patch on the nape. Full body mass and plumage development are not attained until two months of age, at which time the moult of the flight-feathers begins. A further month elapses before the voice and the soft-part coloration typical of adults are acquired.

In the Speckled Mousebird, the young continue to be fed by regurgitation for a month or six weeks after fledging. Food is provided by both parents and helpers, and also, in a significant proportion of cases, by strangers. Juvenile and immature birds spend a lot of time playing in various ways, at times with other individuals, and otherwise with objects such as leaves or twigs. They remain with the parental group for some time, taking part in territory defence and helping with new breeding attempts, but, sooner or later, they usually depart. Dispersive tendencies are clearly greater in females than in males. The former experience a systematic harassment within the group which soon leads to their expulsion, but there is a possibility that some of the young males, perhaps one out of every two or three, remain with the parents for some considerable time and may come to inherit their territory.

Reproductive output among mousebirds is quite low, partly because of the small clutch sizes, but also because of losses from a variety of causes. The noticeable size differences among brood-members, the result of asynchronous hatching, make it more likely that the smallest will die. Many nests are destroyed by wind or rain, with thunderstorms accounting for the loss of about 11% of nests in Gabon. Many others are destroyed by predators, including birds such as coucals (*Centropus*), and reptiles such as certain arboreal snakes; in southern Africa, the predation rate on nests is 23% for Red-faced Mousebirds and 35% for Speckled Mousebirds. The latter species in South Africa has been found to fledge an average of 0.58 young per nest from a mean clutch size of 3.0 eggs, and in Gabon 0.49 young per nest from a mean clutch size of 1.9 eggs. These figures are tantamount to two breeding attempts being necessary, on average, for each young bird which fledges successfully.

On the other hand, mousebirds seem not to be particularly long-lived. Recoveries of ringed birds indicate maximum ages of little more than ten years for the Speckled Mousebird and eight years for the Red-faced Mousebird, while captive individuals have not survived longer than twelve years, figures which are more typical of passerines than they are of non-passerines. The studies of Speckled Mousebirds made by Decoux suggest that population levels of that species are maintained by the relatively rapid succession of breeding attempts. Decoux was able to follow three females over a period of about seven months. He found that two of them made three breeding attempts and the third no fewer than seven, four of those successful, from which he considers that, in the study population, each adult female may lay between four and eight clutches annually. The small size of the eggs and the low number laid in a single clutch imply a relatively modest energetic investment, thereby allowing females to lay replacement clutches only five or six days after a clutch is lost. It also enables a female to lay again some ten to 15 days after successfully fledging young, leaving other individuals of the breeding group to attend to the first brood.

## Movements

The mousebirds, as a group, are undoubtedly highly sedentary birds. Nevertheless, they do exhibit a degree of dispersal or nomadic wandering and, in the case of the genus *Urocolius*, both members of which are superior fliers, even some well-defined seasonal movements. In the austral winter, the Red-faced Mousebird undertakes movements from the dry interior of South Africa to the more humid eastern regions, and there are recovery distances of ringed birds of 31 km and 54 km. Similarly, the Blue-naped Mousebird, in response to clear variations in food availability in Senegal, largely abandons the savannas during the driest months, from December to June, in favour of valley bottoms, where it occupies riverine woodland and gardens. Short-distance altitudinal movements also occur. For example, in Natal, the Red-faced Mousebird moves from interior uplands down to the coast.

In the genus *Colius*, nomadism appears to be more frequent among the two species of the driest habitats than it is among those typical of forest edges, although the available information is sparse. Thus, the White-backed and White-headed Mousebirds perhaps wander somewhat more often than do the Red-backed and Speckled Mousebirds. Observations in Gabon, however, have revealed that transient vagrant or nomadic individuals of the Speckled





Mousebirds build open-cup nests in trees or shrubs and usually lay only two or three eggs per clutch. As many nests fall victim to predation or inclement weather, reproductive output is often very low. The typical nest of the Red-faced Mousebird is placed 2-6 m above ground in a thorny tree and is constructed of a bulky foundation of Acacia twigs and an inner cup lined with fine grasses, mosses, lichens, spiders' webs, wool, feathers and other soft material. Nests have been found throughout the year, but a decided peak in nesting occurs during the austral spring and summer. As visible here, nestlings of the two *Urocolius* species have an odd bulbous swelling on each side of the lower mandible, giving them a somewhat frog-like appearance when they open the mouth to beg for food. Nestlings are brooded almost constantly, even after they have become well feathered, and they are fed by regurgitation. Parent mousebirds swallow the faeces of their young and may feed the droppings back to them, a curious form of coprophagy. The young sometimes leave the nest as early as ten days after hatching, long before they can fly, which no doubt serves to reduce their vulnerability to predation. The usual age for departure is 20 days, after which they may be fed for a month or more by the adults.

[*Urocolius indicus indicus*, near Grahamstown, South Africa.  
Photos: Alan Weaving/  
Ardea]



Mousebird, many of them yearlings, appear among established, territorial breeding groups at the beginning of each rainy season.

### Relationship with Man

Mousebirds tend to be well known to the human inhabitants of the regions which they occupy. This is partly because of the general abundance of these birds and partly because of the frequency with which they visit orchards and gardens. They often receive colloquial names, some of which are onomatopoeic: for example, the Red-faced Mousebird is called "tsivovo" in South Africa and "ohivivi" in Angola, after its characteristic whistling contact call.

The members of the family have a poor reputation, in general, because of the harm which they cause by eating or damaging fruits and vegetables, as well as the buds and flowers of fruiting trees. This damage does not, however, appear to be serious in intensively cultivated areas, since the flocks stay close to woodland and field edges and seldom range far into extensive plantations. In fact, mousebirds pose a greater threat to smallholdings and to ornamental plants. In any event, they are often persecuted directly by farmers, who shoot and poison them, often in large numbers. Mousebirds have also been accidental victims of pesticide applications (see Status and Conservation).

Mousebirds are not very often encountered in captivity. They were first brought to Europe at the end of the nineteenth century, and by 1912 the Speckled Mousebird had been bred in England. Captives reproduce freely, provided they have large aviaries where they can remain in their groups, and so long as they are given suitable plants for perching, climbing and, eventually, nesting. According to several authors, hand-reared mousebirds become very tame and entertaining, given their inquisitive character, their permanent need for company, and their propensity to play with all types of objects. They survive for up to twelve years in captivity.

### Status and Conservation

As a group, the mousebirds are common or very common over much of Africa, and none of the six species is declining or in any way threatened. On the contrary, all are favoured by a diversity of human activities which compensate for the mortality caused by direct persecution, pesticides and roadkills. Man, in effect, continually creates suitable habitats for these birds, as much by his destruction and fragmentation of primary evergreen forest as by his irrigating of previously desertic regions. Indeed, secondary growth, cultivation, especially orchards and fruit plantations, and gardens are ideal mousebird habitats. They are also habitats in which lower predator densities favour improved breeding success. This has been noted in Gabon, where, for the Speckled Mousebird, 58% of nests within villages are successful, compared with 50% on the outskirts and only 36% away from human habitation.

Moreover, the introduction of exotic plants has been advantageous to the Coliidae, by increasing the variety and temporal availability of their food supplies. In Senegal, for example, the recent introduction of the neem tree (*Azadirachta indica*) appears to be responsible for the local increase and spread of the Blue-naped Mousebird.

Apart from the direct persecution which they suffer because of their alleged damage to commercial crops (see Relationship with Man), the mousebirds do not appear to be subject to any major threats from humans. They have, however, been the victims of large-scale pesticide applications aimed at other species. In Senegal, the Red-faced Mousebird is the most frequent non-target species affected by control operations directed against Red-billed Queleas (*Quelea quelea*), the methods employed involving the terrestrial or aerial spraying of fenthion on roosts.

Another common cause of death among mousebirds is collisions with road vehicles. This often happens in the most populated regions of southern Africa, and such mishaps are exacerbated by the birds' tendency to fly in file.

Precise data on population densities are lacking for all but one species. This is the Speckled Mousebird, which occurs at one to two individuals per hectare in Cameroon and two to three birds



per hectare in Gabon. Nevertheless, the abundance levels of nearly all coliiids are described as high or very high in the countries which they inhabit. The scarcest species seems to be the White-headed Mousebird, which is evidently local and rather uncommon in Kenya, the country which spans the central part of its comparatively limited range. The range of the Red-backed Mousebird, which is confined to the Angolan scarp, is more restricted still, but that species is said to be one of the commonest birds there.

In general, the geographical ranges of the mousebirds seem to be stable or expanding. The recent *Atlas of Southern African Birds*, published in 1997, records, for example, various cases of range expansion by coliiids which are more or less clearly related to the spread of agriculture and irrigation, and the same seems to be occurring elsewhere in Africa. Thus, the colonization of new sites by the Speckled Mousebird has been reported from the Karoo, Namaqualand, Lesotho, the southern Transvaal, Zimbabwe, northern Angola, Tanzania and Kenya. Paradoxically, these range extensions could ultimately prove unfortunate from the point of view of the conservation of biodiversity, since they may, by rejoining formerly separate populations, result in the disappearance through hybridization of some of the interesting, well-defined subspecies that currently exist.

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Humans have improved the plight of some mousebirds by creating favourable habitat such as orchards, gardens and second-growth brushland. Indeed, many mousebird populations are expanding in numbers and range owing to the spread of irrigated agriculture. The White-headed Mousebird is a bird of semi-arid areas, but this one is snatching a refreshing drink of water from an irrigation spout. For some mousebirds, however, the presence of agriculture becomes a double-edged sword, when birds are killed because of the damage they allegedly inflict on commercial crops.

[Colius leucocephalus turneri, Kenya.  
Photo: Martin Withers/FLPA]





Subfamily COLIINAE  
Genus *COLIUS* Brisson, 1760

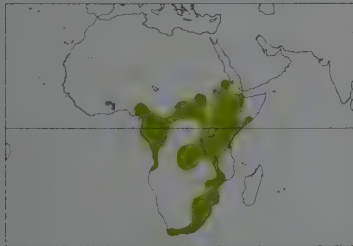
1. Speckled Mousebird

*Colius striatus*

**French:** Coliou rayé      **German:** Braunflügel-Mausvogel      **Spanish:** Pájaro-ratón Común  
**Other common names:** Speckled Coly, Bar-breasted Mousebird/Coly

**Taxonomy.** *Colius striatus* J. F. Gmelin, 1789, Cape of Good Hope. Races can be divided into three groups: “*nigricollis* group” in NW part of range, comprising races *nigricollis* and *leucophthalmus*; “*leucotis* group” of E, including *leucotis*, *hilgeri*, *erlangeri*, *kikuyensis*, *mombassicus*, *jebelensis*, *ugandensis*, *kiwuensis*, *congius*, *cinerascens*, *affinis* and *berlepschi*; and “*striatus* group” of S, with races *simulans*, *rhodesiae*, *integralis*, *minor* and *striatus*. Each group possibly approaching species level, given rare occurrence of hybridization and nearly complete lack of intergradation in contact areas; within groups, however, races often intergrade. Race *erlangeri* often merged with *leucotis*, *ugandensis* sometimes with *kiwuensis*, *berlepschi* with *affinis*, and *integralis* with *minor*. Birds with reddish-brown upperparts and breast from Mt Marsabit and Chyulu Hills, in Kenya, sometimes separated respectively as races *marsabit* and *chyulu*, now generally merged with *kikuyensis*; those from Mt Kilimanjaro, in N Tanzania, previously separated as race *marangu*, but probably a hybrid population and generally placed with *cinerascens*; and those from NW Zambia, described as race *lungae*, now normally included in *congius*. Nineteen subspecies currently recognized.

- Subspecies and Distribution.**
- C. s. nigricollis* Vieillot, 1817 - Ghana (Mole Game Park), and SE Nigeria (E of R Niger and Jos Plateau) E to SW Central African Republic and S to W Angola (Cabinda S to N Namibe) and SW Zaire.
  - C. s. leucophthalmus* Chapin, 1921 - SE Central African Republic, NE Zaire and SW Sudan.
  - C. s. leucotis* Rüppell, 1839 - E Sudan (Blue Nile) and W Ethiopia.
  - C. s. hilgeri* Zedlitz, 1910 - NE Ethiopia, Djibouti and extreme NW Somalia.
  - C. s. erlangeri* Zedlitz, 1910 - SE Sudan and C & SW Ethiopia.
  - C. s. jebelensis* Mearns, 1915 - S Sudan, extreme NE Zaire and N Uganda.
  - C. s. kiwuensis* Reichenow, 1908 - area between L. Albert and L. Tanganyika, in E Zaire, W Uganda, Rwanda and Burundi.
  - C. s. ugandensis* van Someren, 1919 - S Uganda, W Kenya and extreme NW Tanzania.
  - C. s. kikuyensis* van Someren, 1919 - C Kenya Highlands and nearby N Tanzania.
  - C. s. mombassicus* van Someren, 1919 - S Somalia, coastal E Kenya and NE Tanzania.
  - C. s. congius* Reichenow, 1923 - SE Zaire (Kasai Oriental E to L. Tanganyika) S to NE Angola and NW Zambia.
  - C. s. cinerascens* Neumann, 1900 - CN, W & C Tanzania.
  - C. s. affinis* Shelley, 1885 - coastal E Tanzania.
  - C. s. berlepschi* Hartert, 1899 - S Tanzania, NE Zambia and Malawi.
  - C. s. simulans* Clancey, 1979 - extreme S Malawi, and C Mozambique (along R Zambezi valley).
  - C. s. rhodesiae* C. H. B. Grant & Mackworth-Praed, 1938 - highlands of E Zimbabwe and adjacent Mozambique (Manica and Sofala).
  - C. s. integralis* Clancey, 1957 - SE Zimbabwe, S Mozambique (S to Delagoa Bay) and NE South Africa (E Transvaal, NE Zululand).
  - C. s. minor* Cabanis, 1876 - E South Africa (most of Transvaal and Natal), Swaziland and extreme S Mozambique.
  - C. s. striatus* J. F. Gmelin, 1789 - S South Africa (Cape Province E to R Great Kei).



nape, narrow whitish stripe down centre of back, buff borders to wing-coverts, upper mandible greenish or black and lower black to grey, iris usually brown. Races differ mainly in degree of contrast on head, culmen pattern, general tones of plumage, amount of barring, throat colour, leg colour and iris colour, to some extent also in body size: “*striatus* group” upper mandible all black, head sides and crest uniform in colour, legs mostly purplish, all but nominate with blackish throat, *minor* belly washed cinnamon, *integralis* similar but no cinnamon, *simulans* deeper buff below with little or no barring, iris red, *rhodesiae* legs redder; “*nigricollis* group” pale culmen spot, forehead and throat blackish, breast and neck barred, feet red or pink, *leucophthalmus* paler yellow crown, hindneck more strongly barred, iris white; “*leucotis* group” bluish or whitish culmen spot, contrasting pale to whitish ear-coverts, barred to blackish throat, reddish feet, variable iris colour (brown, bluish to whitish, or parti-coloured), *berlepschi* warmer darker brown, throat dusky to blackish, lower throat and hindneck hardly barred, iris brown (sometimes yellowish?), *affinis* paler brown above, face paler, throat light grey with slight mottling, little barring on chest, *mombassicus* crown paler, whitish throat and foreneck distinctly barred, *kikuyensis* generally darker than last, crown and upperparts more red-brown, deeper cinnamon-buff below, face blackish, throat feathers tipped greyish, breast barred blackish, *cinerascens* as previous, but crown much greyer, iris mixed yellow and green-grey, *ugandensis* darker brown above and below, crest somewhat paler than neck, iris yellow to whitish with dark areas in front of and behind pupil, *jebelensis* much paler and greyish, iris yellow, *kiwuensis* very dark brown above and below, throat blackish with conspicuous

white spotting, barring on neck and chest reduced, iris yellow and green-grey, *congius* darkest of all races, very dark greyish-brown, throat and chest unbarred, iris mixed yellowish and grey-green, *leucotis* ear-coverts whitish-buff and less contrasting, throat pale grey, lower throat and foreneck barred, underparts very pale, iris bluish-white, *erlangeri* darker than previous race, ear-coverts whiter, throat blackish, chest and mantle clearly barred, iris bluish-white or greyish, *hilgeri* forehead and throat blackish, ear-coverts brownish-white, chest and hindneck barring very fine.

**Habitat.** Forest edges and clearings, and abandoned cultivations and secondary growth in evergreen forest areas; also many types of open woodland and dense scrub (e.g. thornveld, bushveld), wooded savanna, riparian thickets, hedges around cultivations, and parks and gardens in towns. Avoids closed woodland and open arid areas. Sea-level to 2800 m; to 2500 m in Kenya, 2300 m in Cameroon, 2100 m in S Sudan, 1800 m in Zimbabwe. Where co-occurring with other mousebird species, it tends to occupy comparatively moister areas.

**Food and Feeding.** Mainly fruit, both ripe and unripe, also foliage, buds, flowers, blossoms, nectar, bark; in South Africa, of 12 stomach contents examined, 5 contained only fruit, 5 fruit and foliage, and 2 just foliage. In studies in Gabon, fruits of 22 species detected in diet, mainly *Solanum torvum*, also *Morinda lucida*, *Harungana madagascarensis*, *Rauvolfia*, *Macaranga monandra*, *Ficus*, *Psidium gajava* and others, as well as leaves of 18 species (especially *Dioscorea*, *Carica papaya*, *Morinda lucida*, *Ipomoea involucreata*), the latter taken mainly in evening. In South Africa, fruits of 40 species, flowers of 15 species and leaves of 9 species reported; important among these are *Phoenix reclinata*, *Sideroxylon inerme*, *Ehretia rigida*, *Olea africana*, *Diospyros dichrophylla*, *Euclea*, *Ficus*, *Rhus* and *Lycium*, which also important in diets of *C. colius* and *Urocolius indicus*. Very often eats cultivated fruits (mango, pawpaw) and flowers and shoots of ornamental plants, often causing serious damage. Takes clay-rich earth in association with leaves, also sometimes insects (termites, ants); in Kenya, some birds ate large amounts of cooked and raw meat placed to attract carnivorous mammals.

**Breeding.** Lays throughout year, although seasonal peaks usually apparent: in S Africa in Sept-Jan, with very few nests in other months; in tropical latitudes mainly at end of each dry season (Jan-Mar and Jul-Sept in Gabon, Mar-May and Aug-Sept in Cameroon); during/just after rains in E Africa; same female may lay 4-8 times in a year (in Gabon). Breeds in monogamous pairs, with helpers. Nest a relatively large, untidy open bowl built of a variety of materials (twigs, green stems, leaves, vegetable down, lichens, wool, cotton wool, cobwebs, cloth, paper, string), lined with finer material and very often decorated with green leaves and flowering sprays, placed in bush or tree, most often at height of 2-3 m; often, several active nests close together. Usually 2-3 eggs (average 1.9 in Gabon, 3.0 in S Africa); quite often several females lay in same nest; incubation by both sexes, beginning with first egg, period 10-11 days; nestling with brilliant yellow tongue; may leave nest at 10-11 days, first flights usually at 17-18 days; fed by parents and helpers for up to 1 month after fledging. In Gabon study, 58% of 69 eggs hatched, 77% of chicks fledged, and 77% of fledglings survived for 2 months; in study in South Africa, 39% of eggs hatched and 50% of pulli fledged successfully. First breeding usually after at least 1 year, but possibly occasionally from 6 months. Longevity in captivity usually c. 10 years, but up to 12 years and 4 months.

**Movements.** Highly sedentary, although some movements in Kenya in relation to food availability during dry season, and descending from higher to lower levels in Malawi during non-breeding season. Short-range juvenile dispersal, more marked in females; possibly some nomadism by immatures.

**Status and Conservation.** Not globally threatened. Most widely distributed and perhaps most successful of all mousebirds; widespread and common to very common throughout most of range; nevertheless, distribution seems patchy in some areas, and densities may vary widely. Densities of 1.1-2.0 birds/ha recorded in Cameroon, and 2-3 birds/ha in Gabon. Present distribution has been considerably influenced by man, with cultivations and gardens allowing expansion into formerly unsuitable areas of evergreen forest or arid country; range extensions detected at least in E Karoo, Namaqualand, Lesotho, S Transvaal, Zimbabwe, N Angola, Tanzania and Kenya; expansion may threaten, through hybridization, some presently isolated and well-defined races of this species. Species apparently became extinct on Zanzibar and Pemba, probably during early 20th century, with last apparent record in 1903; reasons of presumed extirpation unknown, and indeed previous presence on these islands is still disputed.

**Bibliography.** Ash & Miskell (1998), Bannerman (1933, 1953), Bartholomew & Trost (1970), Becher (1930), Benson & Benson (1977), Benson *et al.* (1971), Berman (1985), Betts (1966), Bonde (1993), Britton (1980), Brosset & Éraud (1986), Brown, C.R. & Foster (1992), Brown, L.H. & Britton (1980), Bunning (1983), Burger (1982), Cave & Macdonald (1955), Chapin (1929, 1939), Cheesman & Selater (1935), Christy & Clarke (1994), Clancey (1957, 1979, 1996), Cullen, B. (1982), Cullen, R.A. (1988), Cyrus & Robson (1980), Dean (2000), Decoux (1975, 1976, 1978a, 1978b, 1982, 1983, 1985, 1997), Downs *et al.* (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Eiselt (1988), Elgood *et al.* (1994), Etoori & Abe (1992), Filmer (1982), Friedmann (1930a), Fry *et al.* (1988), Ginn *et al.* (1989), Greig-Smith (1976), Grimes (1987), Hamner (1976, 1989b, 1994), de la Harpe (1991), Harrison *et al.* (1997), Hockey *et al.* (1989), Irwin (1981, 1995), Lewis & Pomeroy (1989), Lippens & Wille (1976), Locke (1986), Louette (1981b), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Malbrant & MacLachy (1949), Martin (1998), van der Merwe (1999a), Moltoni (1939), Morceau (1982), (1947), Morel (1974), Newman (1988), Nikolaus (1987), Paget-Wilkes (1928), Penry (1994), Pinto (1983), Prigogine (1971), Prinzing, G. & Prinzing (1985), Prinzing, R. & Schleucher (1996), Rowan (1967a), Rutgers & Norris (1977), Salvan (1972b), Schiffer (1969), Schouteden (1918, 1954, 1963), Short *et al.* (1990), Snow (1978), van Someren (1939), Spence (1973), Steyn (1996b), Tarboton *et al.* (1987), Traylor (1960a), Urban & Brown (1971), Verheyen (1953), Vernon (1970), White (1965), Williams (1994), Yamagishi & Kabango (1985, 1986), Zimmerman *et al.* (1996).

2. White-headed Mousebird

*Colius leucocephalus*

**French:** Coliou à tête blanche      **German:** Weißkopf-Mausvogel      **Spanish:** Pájaro-ratón Cabeciblanco  
**Other common names:** White-headed Coly

**Taxonomy.** *Colius leucocephalus* Reichenow, 1879, Kinakomba, Tana River, east Kenya. Races sometimes merged. Two subspecies currently recognized.

**Subspecies and Distribution.**

- C. l. leucocephalus* Reichenow, 1879 - SE Ethiopia, S Somalia, SE Kenya and adjacent area of NE Tanzania.
- C. l. turneri* van Someren, 1919 - NC Kenya (SE of L. Turkana and Marsabit S to Isiolo District).

**Descriptive notes.** 29-31 cm, including elongated tail of c. 20 cm; 28-42 g (average c. 35 g). Greyish, with creamy-white crown, crest and cheeks, upper back barred black and white; long, graduated tail. Both sexes of nominate race have white streak down back, often concealed by wings;





wings and tail bluish-grey; pinkish-brown throat, vinaceous-buff breast and flanks, pale buff belly, throat and breast lightly barred; blackish-grey orbital skin; upper mandible pale grey with dark tip, lower paler with yellowish tip; legs and feet pinkish-red to coral-red; iris brown. Juvenile white crest, buff throat and breast, bars very faint or absent, bill green above and grey below, legs and feet pale pink. Race *turneri* larger, darker, more heavily barred.

**Habitat.** Dry thornbush vegetation in semi-arid areas, often thickets along watercourses. Usually at altitudes below 1400 m.

**Food and Feeding.** Little information; eats fruits, leaf buds and flowers.

**Breeding.** Laying recorded in Jul in Somalia, in Jun-Aug in Kenya, and in Feb, May-Jul and Nov in Tanzania. Nest an open cup of twigs and pliable material, placed in thick, thorny bush or tree. Probably c. 3 eggs. No other information.

**Movements.** Sedentary; possibly some nomadic and dispersive movements.

**Status and Conservation.** Not globally threatened. Relatively uncommon, with range fragmented in possibly 4 distinct areas; frequent in SE Ethiopia; fairly common and widespread in coastal S Somalia, but absent or nearly so close to Ethiopian border; local and rather uncommon in Kenya.

**Bibliography.** Ash & Miskell (1983, 1998), Bennun & Njoroge (1999), Britton (1980), Brown & Britton (1980), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Friedmann (1930a), Fry *et al.* (1988), Lewis (1984b), Lewis & Pomeroy (1989), Mackworth-Præd & Grant (1957), Moltoni (1939), Schifter (1976, 2000), Short *et al.* (1990), Snow (1978), Urban & Brown (1971), White (1965), Winterbottom (1972a), Zimmerman *et al.* (1996).

### 3. Red-backed Mousebird

#### *Colius castanotus*

**French:** Coliou à dos marron **German:** Rotrückten-Mausvogel **Spanish:** Pájaro-ratón Dorsirrojo  
**Other common names:** Red-backed Coly

**Taxonomy.** *Colius castanotus* J. Verreaux and E. Verreaux, 1855, probably Angola. Monotypic.

**Distribution.** W Angola, from mouth of R Congo E to W Malanje (perhaps to Lunda Norte), and S to Namibe (formerly Moçâmedes).



**Descriptive notes.** 30-38 cm, including elongated tail of 20-26 cm; 39-82 g. Both sexes face and forehead black with whitish-grey feather tips; crest, rest of head, mantle and wings brown, bright chestnut patch on lower back and rump; long, graduated tail brown; sides of head and throat greyish; underparts greyish-brown, slightly vinous on breast, buffy on belly; upper mandible black with grey spot on culmen, lower mandible whitish; feet and toes coral-red to scarlet; upper half of iris yellow, lower portion duller and greener. Differs from rather similar *C. striatus* in bright chestnut on back and rump, no barring on mantle, and on back and rump, no barring on mantle, and on back and rump, no barring on mantle, and on back and rump, no barring on mantle.

throat and breast. Juvenile duller chestnut on rump, pale brown edges to wing-coverts, upper mandible greenish and lower dark, iris dark brown.

**Habitat.** Wide range of habitats, from closed forest and secondary growth to more open wooded areas and clearings, with preference for wooded savanna, forest edge and riverine growth; also thorny scrub, cultivated areas, palm grooves; rarely, in *Brachystegia* woodland. Sea-level to 2000 m.

**Food and Feeding.** Mostly fruits, very often cultivated ones (pawpaw, banana, mango, figs); also flowers, blossoms and green leaves; also, at least occasionally, termites.

**Breeding.** Nests found in Dec and Jan, but birds in breeding condition collected throughout year. Nest bowl-shaped, relatively large, roughly built; in two cases, at height of 3-4 m in tree. Clutches of 1 and 4 eggs recorded; in captivity, once 3 eggs. No other information on breeding. Longevity in captivity 12 years and 3 months.

**Movements.** Sedentary, but local movements to gardens and orchards reported.

**Status and Conservation.** Not globally threatened. Common within its comparatively restricted area, but generally uncommon in S of range; flocks of up to 20 seen in thickets and patches of coastal forest from Bengo S to Benguela town, and foraging parties of up to 12 in clearings in coffee forest at N'Dalatando.

**Bibliography.** Chapin (1939), Dean (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Hall (1960), Lippens & Wille (1976), Mackworth-Præd & Grant (1962, 1970), Pinto (1983), Prinzing (1982a), Prinzing, Göppel & Lorenz (1981), Prinzing, Göppel, Lorenz & Kulzer (1981), Roles (1975), Rutgers & Norris (1977), Schifter (1979), Snow (1978), Traylor (1960a), White (1965).

### 4. White-backed Mousebird

#### *Colius colius*

**French:** Coliou à dos blanc **German:** Weißrückten-Mausvogel **Spanish:** Pájaro-ratón Dorsiblanc  
**Other common names:** White-backed Coly

**Taxonomy.** *Loxia Colius* Linnaeus, 1766, Cape of Good Hope.

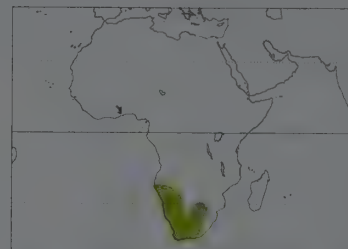
Races intergrade, and are often merged. Two subspecies currently recognized.

**Subspecies and Distribution.**

*C. c. damarensis* Reichenow, 1899 - Namibia and parts of S Botswana S to NW Cape Province and W Transvaal.

*C. c. colius* (Linnaeus, 1766) - Cape Province and W Orange Free State E to W Lesotho.

**Descriptive notes.** 29-32 cm, including elongated tail of 20-23 cm; 38-53 g. Both sexes of nominate race have light grey head, crest and upperparts, narrow white stripe down back flanked by 2 broader black stripes (often concealed by wings), bright maroon patch on rump; long, graduated tail; lores, chin and upper throat dusky to black; buff underparts, vinous on breast; striking black-



and-white pattern on underwing, black band through coverts separating white leading edge from pale grey remiges; bill bluish-white with black tip; legs and feet coral-red; iris blackish-brown. Juvenile no maroon rump patch, paler chin and throat, breast buff, bill bluish-green above and dark grey below. Race *damarensis* paler.

**Habitat.** Wide variety of wooded and bushy habitat types, primarily in semi-arid and arid country; often in riverine belts of trees, hedges around irrigated cultivations, farmyards and suburban gardens.

**Food and Feeding.** Largely fruits, also leaves, flowers and nectar. In South Africa, fruits of 27 species, leaves of 7 species and flowers of 4 species recorded in diet; of 23 stomach contents examined, 13 held only fruit, 5 only foliage, and 7 a mixture of fruit and foliage. In the Karoo, berries of *Lycium* thought to be of especial importance; *Salvadora persica* very important in the Namib Desert; other major food sources include the genera *Phoenix*, *Sideroxylon*, *Ehretia*, *Ficus*, *Rhus*, *Diospyros*, *Euclea* and *Olea*, these also of importance for *C. striatus* and *Urocolius indicus*.

**Breeding.** Lays throughout year, with peak in Sept-Dec and, in most zones, protracted through Jan-Apr. Nest cup-shaped, relatively large, of twigs, stems and grasses, lined with fine grass, vegetable down, cobwebs, wool and feathers, and very often draped with flowering sprays, built 1-2-6 m (most often 1.5-2.5 m) above ground in thick, often thorny tree or bush. 53 clutches averaged 3-1 eggs, but sometimes 2 or more females may lay in same nest; incubation and fledging periods inadequately documented; chick with bright yellow tongue. Of 9 nests, 2 failed because of stormy weather and 1 had infertile eggs. Longevity in captivity 7 years and 7 months.

**Movements.** Sedentary, although some nomadic movements may occur.

**Status and Conservation.** Not globally threatened. Usually common, especially in S half of range; in South Africa, less numerous away from SW arid zone of Cape Province and dry savannas of W Transvaal and W Orange Free State; uncommon to locally fairly common in S Botswana. Range expansion in Transvaal, where first recorded in 1962 in N Johannesburg, and now common there; has possibly expanded also along R Orange. Species benefits from agricultural irrigation and associated settlements, such as orchards, farmyards and gardens.

**Bibliography.** Bunning (1982, 1983), Cade & Greenwald (1966), Clancey (1960b), Cullen, B. (1982), Cullen, R.A. (1988), Day (1987), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Eiselt (1988), Farkas (1966), Fry *et al.* (1988), Ginn *et al.* (1989), Harrison *et al.* (1997), Hockey *et al.* (1989), Hoesch (1955), Lombert & Lukoschus (1981), Mackworth-Præd & Grant (1962), Maclean (1993), Martin (1998), McAllister (1993), McKechnie (1998), van der Merwe (1999b), Newman (1971, 1988), van Nierop (1972), Penny (1994), Rowan (1967a), Sinclair, I. & Davidson (1995), Sinclair, I. & Hockey (1996), Sinclair, I. *et al.* (1993), Sinclair, J.C. (1987), Snow (1978), Steyn (1996b), Tarboton *et al.* (1987), White (1965), Winterbottom (1972a).

## Subfamily UROCOLIINAE

### Genus *UROCOLIUS* Bonaparte, 1854

### 5. Blue-naped Mousebird

#### *Urocolius macrourus*

**French:** Coliou huppé **German:** Blaunacken-Mausvogel **Spanish:** Pájaro-ratón Nuquiazul  
**Other common names:** Blue-naped Coly

**Taxonomy.** *Lanius macrourus* Linnaeus, 1766, Senegal.

Genus often merged into *Colius*. Forms a superspecies with *U. indicus*. Race *syntactus* often merged with nominate, and *laeneni* sometimes included too. Seven subspecies currently recognized.

**Subspecies and Distribution.**

*U. m. macrourus* (Linnaeus, 1766) - coastal SW Mauritania and Senegal; recorded also in Gambia and Guinea-Bissau.

*U. m. syntactus* (Oberholser, 1905) - Sahelian and Sudanese zones from Mali, S Niger and N Nigeria E to Sudan, Eritrea and N Ethiopia.

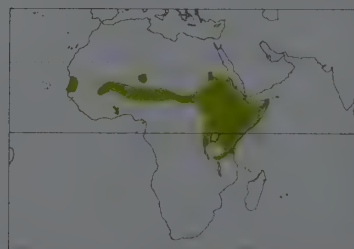
*U. m. laeneni* (Niethammer, 1955) - Air Massif, in NC Niger.

*U. m. abyssinicus* Schifter, 1975 - C & S Ethiopia, and N Somalia (S to about Beledweyne).

*U. m. griseogularis* van Someren, 1919 - S Sudan, E Zaire, W Uganda, Rwanda, Burundi, and NW & (probably this race) SW Tanzania; this race sometimes said to occur in SW Ethiopia.

*U. m. pulcher* (Neumann, 1900) - extreme SE Sudan, E Uganda, Kenya, S Somalia and N Tanzania.

*U. m. massaicus* Schifter, 1975 - C & E Tanzania (E to near Dar-es-Salaam).



**Descriptive notes.** 33-36 cm, including elongated tail of 20-28 cm; 34-58 g. Ash-grey plumage, darker above than below, bright turquoise-blue patch on nape and hindneck, long crest; very long, slender and steeply graduated tail, female's shorter than male's. Both sexes nominate race brown-tinged ash-grey above, greyish-buff below; bare skin on lores and around eyes crimson-red; most of upper mandible crimson-red, rest of bill black; feet purplish-red. Juvenile no blue nape patch, shorter crest, pink facial skin, greenish bill. Race *syntactus* paler, more yellowish than nominate, *laeneni* smaller and even paler; E races ("pulcher group") somewhat darker, bluish/greenish wash on wings and tail, *pulcher* with reddish tinge on breast, *abyssinicus* with whiter throat and darker breast than previous, *griseogularis* darker with vinous wash on throat and breast, *massaicus* paler and greyish.

**Habitat.** Open woodland and bush in semi-arid country, including thornbush, savanna, open *Acacia* woodland; frequents bushes along watercourses and wells, date-palm groves, farms, outskirts of villages and towns, and gardens. Sea-level to 1900 m in Kenya, where typically below



1600 m, to 2100 in Ethiopia. Where sympatric with *Colius striatus*, it tends to occupy the drier habitats.

**Food and Feeding.** Mainly fruits, supplemented with leaves, flowers and buds. Berries of *Salvadora persica* of supreme importance in some areas (Niger, Chad); other plants exploited include *Balanites aegyptiaca*, *Capparis decidua*, *Boscia senegalensis*, *Grewia villosa*, *Tamarindus* and *Ficus*, as well as dates and many other cultivated fruits.

**Breeding.** Throughout year, with peaks varying regionally, typically in or just after rainy seasons: in May-Jun in Nigeria, May-Jun and Dec-Feb in N Sudan, and Mar-Jun in Zaire. Nest a shallow cup of twigs, scantily lined with grass and rootlets, placed in tree or thorny bush. Usually 2-3 eggs; incubation c. 11 days; chick has peculiar bulbous swellings at base and on both sides of lower mandible; young may leave nest at 10-11 days, first flights at 16-17 days. Longevity in captivity up to 11 years and 5 months.

**Movements.** Sedentary or locally nomadic. At least in Senegal, Mali, Kenya and Tanzania, regular dry-season movements take place from savanna woodland to river valleys and built-up areas; rare observations of the species from Gambia and Guinea-Bissau are probably the results of such movements.

**Status and Conservation.** Not globally threatened. Widespread and fairly common to common, or locally abundant, throughout most of range from Senegal to Ethiopia and Kenya; very common and widespread in Somalia, although some inexplicable and often large gaps in distribution there; now uncommon in N Nigeria, where decrease in population noted in Kano State since at least 1970's. Apparently expanding in Senegal, where benefits from extensive planting of introduced neem tree (*Azadirachta indica*); also in Senegal, identified as particularly at risk during operations aimed at controlling populations of Red-billed Queleas (*Quelea quelea*), roosts of which are sprayed with fenthion.

**Bibliography.** Abt (1995), Ash & Miskell (1998), Bannerman (1953), Barlow *et al.* (1997), Bates (1927), Betts (1966), Britton (1980), Brown & Britton (1980), Butler (1905, 1908), Cave & Macdonald (1955), Chapin (1939), Cheesman & Schlater (1935), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Eiseelt (1988), Elgood *et al.* (1994), Faïron (1975), Finke *et al.* (1995), Friedmann (1930a), Fry *et al.* (1988), Gibson (1979, 1980), Giraudoux *et al.* (1988), Gore (1990), Heim de Balsac & Mayaud (1962), Lauterbach & Prinzinger (1994), Lewis & Pomeroy (1989), Lippens & Wille (1976), Mackworth-Praed & Grant (1957, 1970), Moltoni (1939), Morel (1968, 1974), Mullié *et al.* (1999), Niethammer (1955), Nikolaus (1987), Paludan (1936), Prinzinger (1988), Prinzinger & Roth (1987a, 1987b), Prinzinger & Schleucher (1996), Prinzinger, Finke & Dietz (1993), Prinzinger, Misovic & Kleinschmidt (1994), Prinzinger, Schleucher & Preßmar (1992), Salvan (1968), Schaub & Prinzinger (1999), Schaub *et al.* (1999), Schifter (1969, 1975, 1986), Schouteden (1954), Short *et al.* (1990), Snow (1978), Snow & Perrins (1998), Urban & Brown (1971), White (1965), Zimmerman *et al.* (1996).

6. Red-faced Mousebird

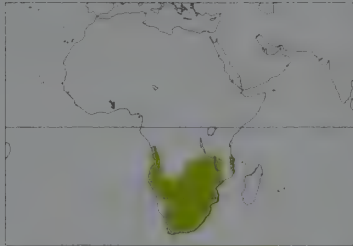
*Urocolius indicus*

**French:** Coliou quiriva      **German:** Rotzügel-Mausvogel      **Spanish:** Pájaro-ratón Carirrojo  
**Other common names:** Red-faced Coly

**Taxonomy.** *Colius indicus* Latham, 1790, India; error = Gamtoos River, Cape Province. Genus often merged into *Colius*. Forms a superspecies with *U. macrourus*. W Angolan population has been separated as race *angolensis*, but now usually regarded as indistinguishable from *lactefrons*; birds from SE Zaire sometimes assigned race *luababae* and those of N Botswana race *ngamiensis*, but both probably better included within *mossambicus*. Five subspecies currently recognized.

**Subspecies and Distribution.**

- U. i. lactefrons* (Sharpe, 1892) - coastal Angola (S from Cabinda) and most of Namibia.
- U. i. mossambicus* (Reichenow, 1896) - extreme SE Zaire and SW Tanzania (around L. Rukwa) S to SE Angola (N possibly to E Mexico). Zambia and Malawi.
- U. i. pallidus* (Reichenow, 1896) - coastal areas of extreme SE Tanzania and N Mozambique.
- U. i. transvaalensis* (Roberts, 1922) - SW Zambia, Zimbabwe and S Mozambique S to South Africa (except S).
- U. i. indicus* (Latham, 1790) - S Cape Province E to R Great Kei.



**Descriptive notes.** 29-37 cm, including elongated tail of 19-25 cm; 45-65 g. Grey upperparts with greenish metallic sheen, especially on wings and tail, buff below; tail very long and slender, sharply graduated. Both sexes of nominate race dark ashy blue-grey above, including crest; buff forehead, tawny-buff below; underside of wings and tail chestnut; bare skin on lores and around eyes carmine-red; most of upper mandible carmine-red, rest of bill black; feet dark purplish-red; iris yellow to dark brown. Differs from *U. macrourus* in darker coloration, buff forehead, no blue patch on nape. Juvenile crown and ear-coverts buff, buff

edges to wing-coverts, bare orbital skin and base of bill greenish, feet duller, iris brown. Races differ mainly in intensity of plumage colour: *mossambicus* dark and rather large, *pallidus* paler and tinged pink below, *transvaalensis* less blue-toned with brownish-cream forehead, *lactefrons* palest with creamy-white forehead.

**Habitat.** Typically savanna woodland, frequenting wide range of scrub, bush and wooded habitats, avoiding only dense forest and open grassland; common in riverine thickets, palm groves, orchards and gardens.

**Food and Feeding.** Mostly fruits, also leaves, buds, flowers and nectar; in South Africa, examination of 24 stomach contents gave 11 with only fruit, 5 with only foliage, and 5 with mixed fruit and foliage. Important plant genera, as for *C. striatus* and *C. colius*, include *Lycium*, *Phoenix*, *Sideroxylon*, *Ehretia*, *Ficus*, *Rhus*, *Diospyros*, *Euclea* and *Olea*; *Salvadora persica* a very important food in the Namib Desert. Cultivated and exotic plants extensively exploited, such as mulberry and vines in Zimbabwe.

**Breeding.** Nests found throughout year, but marked peak in austral spring/summer: Sept-Apr in Angola, Aug-Dec in Zambia, Sept-Dec in Zimbabwe, Sept-Jan in most of S Africa but Aug-Oct in coastal Cape Province. Nest an untidy open bowl with large foundation of dry twigs, usually branched and thorny (often of *Acacia karoo*), and finely lined cup of variety of softer material including grass, moss, vegetable down, lichens, cobwebs, feathers, wool, paper, placed in thorny tree or bush at height of 1-3-6 m (average 3 m). 150 clutches averaged 2-6 eggs, but several females may lay in same nest; incubation by both sexes, beginning with first egg, c. 13 days, in captivity 12 days recorded; chick with peculiar bulbous swellings at base and on both sides of lower mandible; may leave nest when 10 days old, fledges at c. 20 days. Longevity in captivity up to 12 years and 5 months.

**Movements.** Sedentary or locally nomadic; irruptions in dry season or during droughts detected in several areas, as well as altitudinal movements during non-breeding season in Natal. Most recoveries of ringed birds within very short radius from ringing site, but one at 31 km and another at 54 km.

**Status and Conservation.** Not globally threatened. Widespread and common in South Africa and Botswana; widespread but usually sparse and local in Zambia; very common in SW Angola; locally common in Malawi and S Mozambique. As with other members of the Coliidae, distribution appears to be influenced by the presence of suburban gardens, fruit farming and irrigated agriculture; considerable increases were reported in both Namibia and Zimbabwe during 1940's and 1950's, but atlas work shows no substantial changes in any part of S Africa since c. 1970's. In South Africa, possibly some decreases along R Orange, where *Colius colius* is now more common than present species.

**Bibliography.** Aspinwall (1992a), Baker (1994), Benson & Benson (1977), Benson *et al.* (1971), Bonde (1993), Bunning (1982, 1983), Cade & Greenwald (1966), Clancey (1960a, 1996), Clarke (1904), Cullen (1988), Cyns & Rohson (1980), Dean (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Earlé & Grobler (1987), Eiseelt (1988), Every (1983, 1988), Farkas (1966), Fry *et al.* (1988), Ginn *et al.* (1989), Hanmer (1994), Harrison *et al.* (1997), Herremans & Herremans-Tonnoeyr (1994a), Hockey *et al.* (1989), Hoesch (1955), James (1948), Kemp (1974), Lippens & Wille (1976), Macek & Bohmke (1994), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Markus (1964), Newman (1968, 1988), Penry (1994), Pinto (1983), Rowan (1967a), Schifter (1966, 1967b, 1978), Schoonees (1963), Schouteden (1954), Short *et al.* (1990), Snow (1978), Steyn (1971, 1996b), Taher (1994), Tarboton *et al.* (1987), Taylor (1997), Traylor (1965), Tyler (1997), White (1965), Winterbottom (1971), Yamazaki *et al.* (1986).





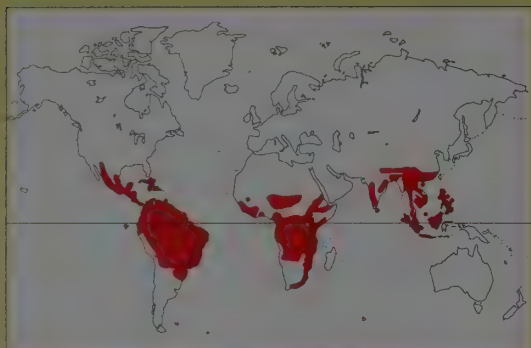
# Order TROGONIFORMES

## Trogoniformes

Trogonidae

trogons

Class AVES  
Order TROGONIFORMES  
Family TROGONIDAE (TROGONS)



- Compact, short-necked arboreal birds with long, graduated tail, short wings, short, broad, hooked bill, and very short legs; plumage brightly coloured.
- 23-40 cm.



- Almost pantropical (absent from Australasian Region).
- Forest.
- 8 genera, 39 species, 107 taxa.
- No species threatened; none extinct since 1600.

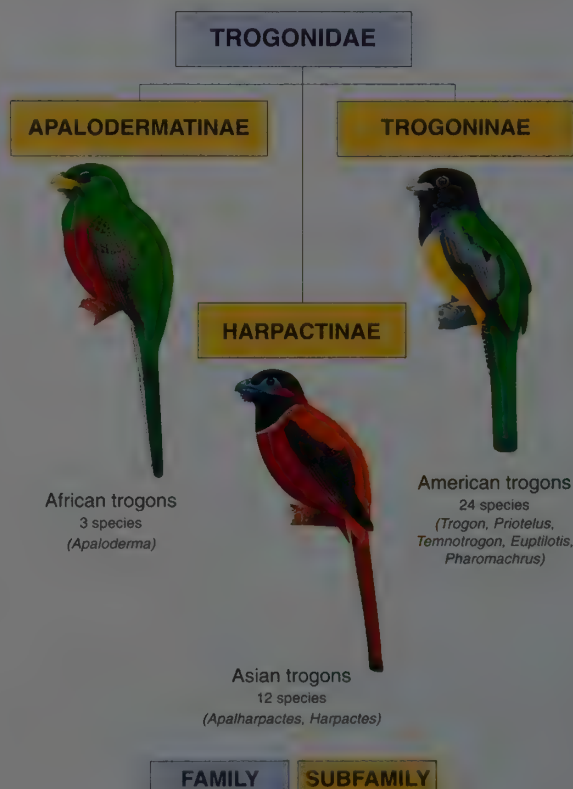
### Systematics

Considering its very wide global distribution, Trogonidae is a distinctive and yet remarkably uniform family. It has always been placed in the vicinity of the cuckoos (Cuculidae), parrots (Psittacidae), toucans (Ramphastidae), puffbirds (Bucconidae), jacamars (Galbulidae) and rollers (Coraciidae), and often near the owls (Strigidae), nightjars (Caprimulgidae) and swifts (Apodidae), the turacos (Musophagidae) and the motmots (Momotidae). Recent studies of various attributes, including musculature, bones, feeding apparatus, fossils and biochemistry, have combined to support the long-held assumption that Trogonidae might best be considered part of the Coraciiformes, although it is still very unclear with which families within that complex order it shows the strongest affinities. Moreover, it would appear evident, if only from the unique arrangement of their toes, that the trogons possess no close living relatives, so that for the time being it may be most appropriate to treat them in their own order, Trogoniformes. This seems particularly apposite given that the most recent biochemical work, by A. Espinosa de los Monteros in 1998, using mitochondrial cytochrome-*b* and 12S ribosomal RNA gene sequences, has suggested that the closest surviving relatives of the trogons are the mousebirds (Coliiformes), an exclusively Afrotropical order.

In the past, centres of diversity of species have been reckoned to indicate their geographical origins. That this is no longer an acceptable assumption is well illustrated by the trogons. Despite the fact that two-thirds of all living trogon species, 25 out of 39, are Neotropical, the DNA evidence that places them near the mousebirds suggests, unsurprisingly, that it is Africa, with its mere three species, that represents their ancestral home, with *Apaloderma* emerging as the most primitive trogon genus, the other forms branching off between 36 and 20 million years ago. Evidence supporting an African origin includes the fact that the oldest trogoniform fossil derives from Tertiary deposits in Europe: an undescribed heterodactyl from London Clay (Essex) dating back to the Lower Eocene, as many as 53 million years ago. Moreover, there is *Protornis glarniensis*, from Middle Oligocene rock in Switzerland, and *Paratrogon gallicus*, from the Lower Miocene in France. In the New World, the oldest known fossils as yet are from the Pleistocene.

In their influential 1990 treatment of avian systematics, C. G. Sibley and B. L. Monroe recognized 39 living species of trogon in six genera and two subfamilies. These were the subfamily Apalodermatinae, with three species in the single genus *Apaloderma*, and the subfamily Trogoninae. The latter was bro-

ken into two tribes: Trogonini, containing five species in the genus *Pharomachrus*, one in *Euptilotis*, two in *Priotelus*, and 17 species of *Trogon*, and the tribe Harpactini, with 11 species all placed in the genus *Harpactes*. The counterintuitive feature of this arrangement is that it unites in one subfamily two tribes that are separated not only by a massive distance geographically, but also by the other subfamily, although it is possible that the New World could initially have been colonized from Asia via Siberia and Alaska. Espinosa de los Monteros appeared to revise this unhappy circumstance by suggesting that Asian *Harpactes* is the closest relative of *Apaloderma*, leaving the New World genera as the most recently derived assemblage, splitting off some 33-18 million years ago; yet he did not alter Sibley and Monroe's



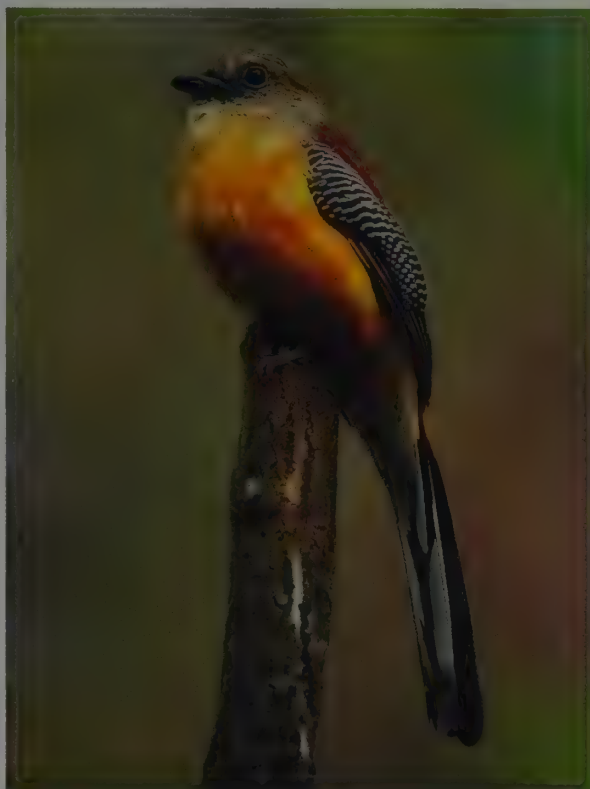
Subdivision of the  
Trogonidae

[Figure: Richard Allen]

Most Asian trogons have rather similar black, red and cinnamon plumage in males, with more browns and greys in the females. The exception in *Harpactes* is the Orange-breasted Trogon, with its yellow and orange underparts and green head. Far more distinct, however, are two species which are now separated in the genus *Apalharpactes*.

The Sumatran (*Apalharpactes mackloti*) and Javan Trogons have a red bill, green upperparts, a grey-green band on the breast and an iridescent blue-green tail; also, the Sumatran possesses a remarkable vocalization. Hitherto, the two have been regarded as conspecific, but differences in overall size, bill size, tail length and rump colour suggest that they should be treated as two distinct species.

[Left: *Harpactes oreskios*.  
Right: *Apalharpactes reinwardtii*.  
Photos: Dieter Hoppe]



subfamily arrangement. Independent work by U. Johansson, published in 1998, has suggested, by contrast, that the African and Asian trogons are very close, while the New World forms are separated from both by several characters which could be explained by their early divergence and distant relationship. For the present, it would seem reasonably practicable to divide the Trogonidae into three subfamilies on the basis of their geographical distribution, although it has to be admitted that this is a solution designed merely for convenience.

Notwithstanding the studies mentioned above, the African and the American trogonids in some respects appear to be far closer to each other than either group does to those from Asia. In the first two, the upperparts and, in the case of males, the breast, too, are metallic green, while some species have barred outer tail feathers; in Oriental *Harpactes*, the upperparts of both sexes are brown and the tail is never barred. Direct comparison of a specimen of the Bar-tailed Trogon (*Apaloderma vittatum*) from Central Africa with one of the Blue-crowned Trogon (*Trogon curucui*) of the central South American subspecies *peruvianus* reveals a remarkable degree of homogeneity: the upperparts are virtually identical, Bar-tailed having a bluer uppertail and *peruvianus* a bluer crown and more densely barred wing-panel, and both have a pale bill, a black throat shading to blue breast, the latter green-centred on Bar-tailed, as well as bright pinkish-red underparts with a richly barred black-and-white undertail. How two such lookalikes could be separated by tens of millions of years, or be farther apart than *Apaloderma* is from *Harpactes*, remains a matter of exclamation. It is hardly surprising that some taxonomists have suggested that the entire family could be treated within just two genera, *Trogon* and *Pharomachrus*. Although perhaps unfashionable, the retention or resuscitation of several genera highlights the most anomalous taxa, which may hold the key to understanding the evolutionary history of the three main groupings but which have apparently been overlooked in recent analyses.

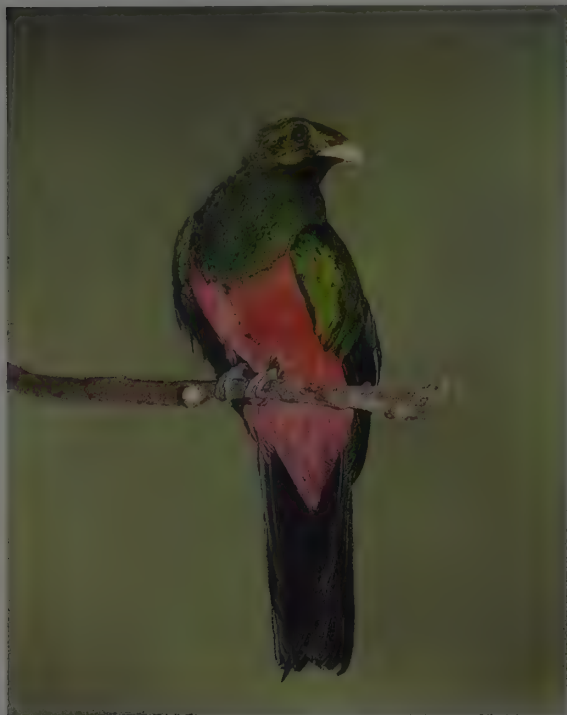
One important way in which African *Apaloderma* differs from Neotropical *Trogon*, and indeed from all New World trogonids, is in its patches of coloured bare skin below the eye. This aspect certainly suggests a link to Oriental *Harpactes*, in which the coloration of the bill and bare facial areas are major characters. The three African species appear to be monophyletic. The genus *Heterotrogon*, sometimes used for the Bar-tailed Trogon, was

established mainly on the basis of the smallness and less serrate form of the bill, but, as in *Trogon*, neither this nor the barring of its outer tail feathers is a character of real generic significance; on the other hand, that species does differ to some extent from the other two African trogons in its vocalizations (see Voice).

The Asian trogons are a distinct assemblage, but they may not be entirely monophyletic. All but three are ostensibly related on the basis of recurrent patterns generally combining yellowish-brown upperparts, chestnut-brown tail with black edging or terminal bar, red or yellow belly, red or black head and blue-edged bill. One of the three non-conformers, Ward's Trogon (*Harpactes wardi*) has a pink bill and plain tail, but is otherwise recognizably a *Harpactes*. The other two, however, are the only Asian trogons to show metallic tones in the plumage, in addition to which they have a red bill, green upperparts and yellow underparts, and the tail is blue; it is the latter that possesses the metallic sheen. On this basis, and because at least one of them is known to have a song quite unlike that of any other trogon (see Voice), it seems reasonable to separate them in the resurrected genus *Apalharpactes*, the combination of *Apalo-* and *Harpactes* suggesting what may be a real link to the African trogons. Furthermore, the two taxa have usually been combined as subspecies of a single species under the name of "Blue-tailed Trogon", but recent research, as yet unpublished, indicates that they should probably be treated as separate species, namely, the Sumatran Trogon (*Apalharpactes mackloti*) and the Javan Trogon (*Apalharpactes reinwardtii*). The two populations evidently differ significantly in biometrics, while it is the former that has the above-mentioned unusual song, although the song of the Javan Trogon appears not to have been described.

In the New World, the greater number of species, coupled with the subtleties of many of their characters, has left a more complex situation which remains to be unravelled by a robust theory. If exclusive insectivory is assumed to be the primitive condition of the family, as shown by the genus *Apaloderma*, then high levels of frugivory such as are exhibited by the quetzals (*Pharomachrus*) must be a later specialization that arose as the birds colonized colder montane regions, where invertebrate biomass would be expected to decline. Biochemical analysis suggests that the Caribbean trogons are the most primitive species in the New World, but it also indicates their links to the quetzals, a





circumstance certainly borne out by morphological comparisons but one which contradicts the notion of their primitive state.

It is considerably easier, recalling the alignment of African *Apaloderma vittatum* and Neotropical *Trogon curucui peruvianus*, to regard *Trogon* as the most primitive genus in the Americas. This large assemblage traditionally breaks down into several subgenera which formerly served as full generic divisions. The subgenus *Trogon* applies to species with a graduated tail and which produce young essentially coloured like the adult female. These are Baird's (*Trogon bairdii*), the White-tailed (*Trogon viridis*), the Black-headed (*Trogon melanocephalus*) and the Citreoline Trogons (*Trogon citreolus*) and, perhaps, the Surucua Trogon (*Trogon surrucura*). The subgenera *Chrysotrogon* and *Trogonurus* gather together the smaller, slighter species with relatively weaker bills. *Chrysotrogon*, represented solely by the Violaceous Trogon (*Trogon violaceus*), has a short tail, largely feathered tarsi and adult-like young. *Trogonurus*, comprising the Mountain (*Trogon mexicanus*), Elegant (*Trogon elegans*), Masked (*Trogon personatus*), Collared (*Trogon collaris*), Black-throated (*Trogon rufus*) and Blue-crowned Trogons, has half-feathered tarsi and a long tail, and the young, unlike the adults, are conspicuously spotted. This last character is shared with the subgenus *Curucujus*, which unites the final four species, the Slaty-tailed (*Trogon massena*), Black-tailed (*Trogon melanurus*), Lattice-tailed (*Trogon clathratus*) and White-eyed (*Trogon comptus*). All of those four have the toes more fused and the tail less strongly graduated; moreover, they are more frugivorous than other *Trogon* species, and this trait parallels their more quetzal-like body size and plumage, lacking as they do both tail-barring and a prominent white breastband.

This arrangement is not well supported by biochemical evidence. In DNA studies, *Trogon* broke down into two subclades. One, the *violaceus* subclade, with the taxa *violaceus*, *curucui* and *viridis* and, at a greater distance, *comptus* and *melanurus*, is composed chiefly of termitarium-nesting species which make upsloping tunnels and spacious hidden chambers. The other, the *elegans* subclade, with the taxa *elegans*, *rufus*, *collaris*, *personatus* and, at a greater distance, *mexicanus*, is composed predominantly of shallow tree-cavity nesters which leave themselves largely visible while incubating. Within the latter, however, the Elegant Trogon may have lost the excavating behaviour altogether, while the Collared Trogon has developed termitarium-nesting habits in the north-east of its range, although its nests are still shallow and exposed in the manner of those of cavity-makers of its subclade.

The *Pharomachrus* quetzals are characterized by the uppertail-coverts extending to or beyond the tip of the tail, the median wing-coverts projecting up to or over the line of the closed wing, and the loreal feathers being closely adpressed. The genus presumably arose in the Andes and radiated into the Caribbean coastlands, the Amazon lowlands and the Central American isthmus in the Pliocene, in the immediate wake of the Lauraceae, on which its members are so heavily dependent. Thus, the Resplendent Quetzal (*Pharomachrus mocinno*), with its most spectacular plumage, emerges as the most recent of the genus. *Euptilotis* has recently been argued to be a quetzal on the basis of its voice and the pale blue, rather than white, egg colour, and this hypothesis has been strongly supported by DNA work. The single species in the genus, the Eared Quetzal (*Euptilotis neoxenus*), has the uppertail-coverts extending half-way down the tail in the male, and both sexes have feathered eyelids, with the feathers behind the eye and on the ear-coverts produced into long hair-like filaments, hence "*Euptilotis*"; the bill is proportionately slender, reflecting in part the loss of the excavating habit of the family. Both *Pharomachrus* and *Euptilotis* have lost the distinctive trogonid wingpanel. Both genera, however, have spotted young, which aligns them with the subgenera *Curucujus* and *Trogonurus*; it is worth noting that this appears to be a derived character, since *Apaloderma* produce adult-like young.

This leaves only the two most anomalous Neotropical trogons, from Cuba and Hispaniola respectively. Trogons are evidently extremely poor long-distance dispersers, to judge from their absence elsewhere from all but land-bridge islands, so their presence on the largest islands in the Caribbean suggests a very ancient lineage. It seems likely that, as J. Bond thought, they are of common ancestry, given the similarities of their underparts and the white notches on the outer webs of their primaries. To treat them as congeneric, however, as some modern authors have done, perhaps overplays their proximity. The curious characters of the Cuban Trogon (*Priotelus temnurus*), which include its grey and pink bill, bold blue cap and white throat, extensive white markings on the wings, absence of a wingpanel, absence of sexual dimorphism, and excised tips of the tail feathers, may all be mere secondary modifications; and this may even be true of the tongue, with its split tip, evidently associated with its flower-feeding habit. Nevertheless, these factors in combination suggest that the Cuban taxon is sufficiently evolved from its neighbour the Hispaniolan Trogon (*Temnotrogon roseigaster*), which, incidentally, has a normal tongue, to enjoy separate generic status. Certainly, if *Apaloderma vittatum* and *Trogon curucui peruvianus* belong to different genera, there would appear no reason not to retain both *Temnotrogon* and *Priotelus*.

It is also noteworthy that female *Temnotrogon* is very similar in appearance to female *Euptilotis*. It may well be that the characters of continental male trogons have been lost in the Caribbean, such a development being a common characteristic of island endemics, and that the white spotting in the wings represents a modified retained juvenile character, another insular tendency. The loss in *Priotelus* and in female *Temnotrogon* of the typical trogonid wingpanel suggests a further link to the quetzals, as does those species' highly frugivorous habit. More interesting still is the fact that these three genera share feathered eyelids and the hair-like filaments produced from the ear-coverts. On this basis it may be postulated that the quetzals are a derivation of *Trogon*, and that the Central American *Euptilotis* and the Caribbean *Priotelus* and *Temnotrogon* represent an early radiation of quetzal-type birds. This does, of course, result in the position that *Priotelus* is among the most derived of the Trogonidae, diametrically the opposite of recent DNA studies; yet intuitively this makes some sense.

## Morphological Aspects

The trogons are compact-bodied, short-necked and mid-sized birds, 23-40 cm in length discounting any tail-streamers. They are essentially arboreal, coming to ground only when seizing a prey animal, but they are incapable of walking, although a Bar-tailed Trogon has been seen "to run up a tree-trunk almost like a woodpecker", and a Narina Trogon (*Apaloderma narina*) to shuffle along

The Golden-headed Quetzal forms a superspecies with the Pavonine Quetzal (*Pharomachrus pavoninus*), and the two have often been considered conspecific. The Golden-headed's golden head is a notable feature, but perhaps the most striking difference is in bill colour, the male Golden-headed's being yellowish whereas the male Pavonine's tends to be orange-red at least around the base and often much more, typically with a paler or darker tip. The bills of the respective females are greyish to brownish, and reddish with a variable dark tip.

[*Pharomachrus auriceps*. Photo: Josep del Hoyo/Lynx]

It seems likely that the two most atypical Neotropical trogonids, the Cuban Trogon and the Hispaniolan Trogon (*Temnotrogon roseigaster*), possess a common ancestry, dating back to the time when their respective islands were connected by a land-bridge to mainland America. They have often been lumped in the same genus, *Priotelus*, as they share certain features, notably the red belly and the white markings on the outer webs of the primaries, but in many other respects the Cuban Trogon is strikingly different from its Hispaniolan relative, for instance in its dark violet-blue head, its white throat, and its pink and grey bill. It is, however, the peculiar tail shape that catches one's attention: the central rectrices end in ragged tips, while the white lateral feathers protrude at the outer edge to produce a curious ratchet effect, this being particularly noticeable when the tail is viewed from below. The special tongue with its split tip, a feature evidently closely associated with this species' predilection for feeding on flowers, the lack of the typical trogonid wingpanel, and a total absence of sexual dimorphism, together with other singularities, all combine to suggest that the Cuban Trogon has diverged more than sufficiently from its near neighbour on Hispaniola to merit generic separation. Known as the "tocoloro" in Cuba, on account of its song, this species has been chosen as the national bird of the island, since its red, white and blue plumage reflects the colours of the Cuban flag.

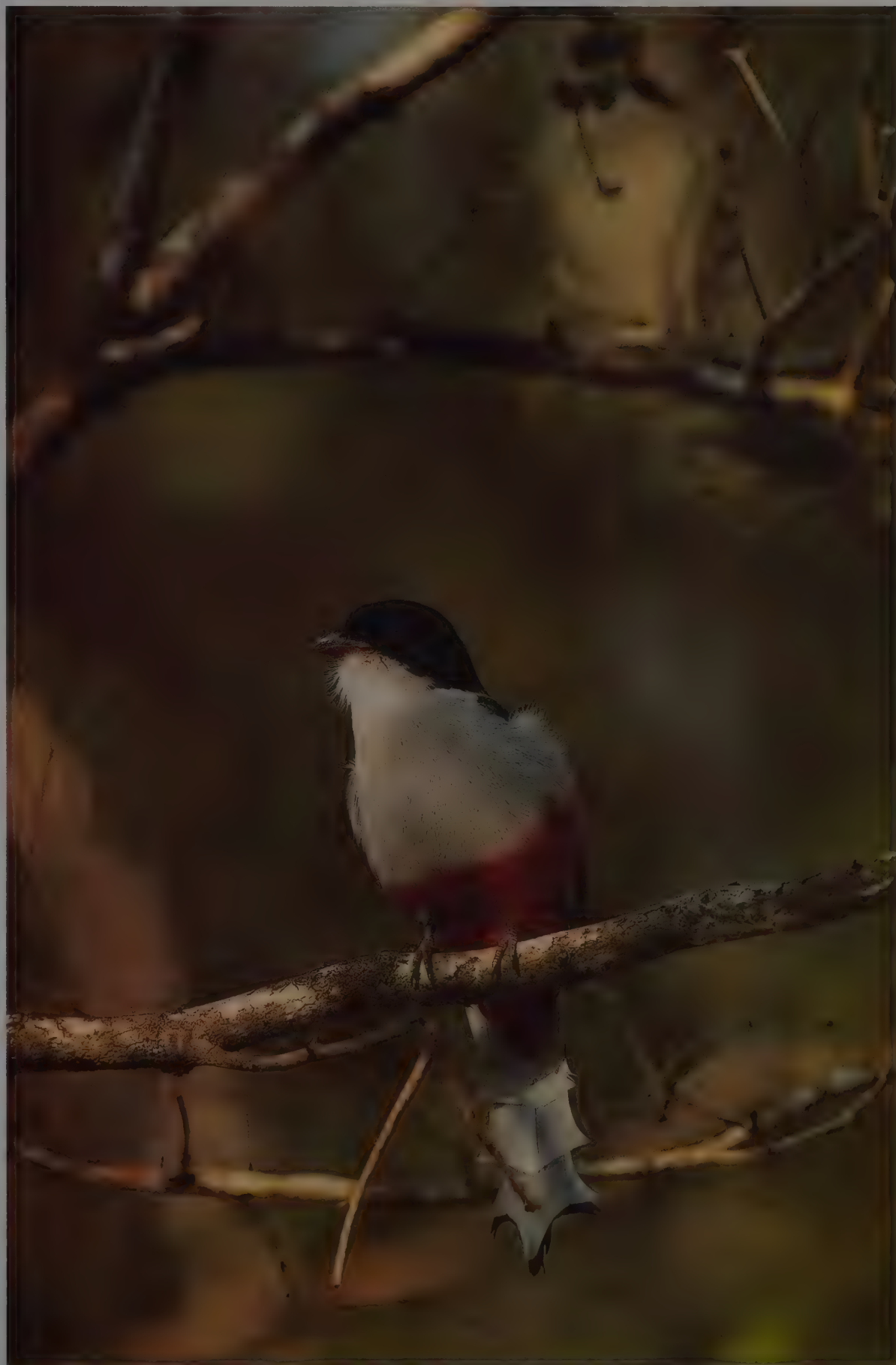
[*Priotelus*

*temnurus temnurus*,

Ciénaga de Zapata, Cuba.

Photo: Doug Wechsler/

VIREO]





branches. Indeed, their foraging strategy, typified as "perch-and-pounce", "still-hunting", "sally-gleaning", and so on, is strongly reflected in their morphology. The bill is short, broad, hooked and strong, the wings are short, rounded and strongly arched, the tail is long, broad and squared-ended, with pronounced but concealed graduation, and the legs are very short, the largely feathered tarsus being shorter than the longer leading toe. These are all features which combine to provide considerable advantages in terms of aerial manoeuvrability, secure prey capture and between-flight stillness.

Neotropical trogonids exhibit a ratio of flight muscle to body weight of about 22%, slightly higher than that of the parrots. On the other hand, their ratio of leg muscle to body weight, about 3% in seven species, is the lowest of all species sampled and only half that of most, indicating the striking irrelevance of the legs and feet in trogon locomotion. Trogons' legs are in fact so undeveloped that the birds are unable to turn around on a perch without using their wings.

Nevertheless, it is the branch-gripping feet that are the trogons' single most distinctive character. Like the parrots, cuckoos, woodpeckers (Picidae) and others, they have the toes in pairs, and are to that extent zygodactylous. They differ, however, in having the inner instead of the outer toe reversed, so that the hallux, the normal hind toe, is the outer of the two hind toes, whereas in all other zygodactyl birds it is the inner one. This "heterodactylous" condition is correlated with a unique arrangement of the deep plantar tendons, the front of which (*flexor perforans*) is split in two and leads to the two front toes, while the rear one (*flexor hallucis*) is also split and leads to the two back toes.

Another distinctive feature of trogons is their thin skin, which is evidently the reason why their feathers so easily detach from the body, although this is not unique among birds, since nightjars and some pigeons (notably *Streptopelia*) present the same condition. The literature is full of complaining asides by museum collectors on the difficulties of preparing trogon specimens. To begin with, many of the feathers fall out as the shot bird tumbles to the ground; and later, when the specimen is laid out on the preparing table, the skin proves "about as stout as wet tissue paper", more feathers are lost, the legs often come away, and the bird commonly ends up as misshapen as a roadkill. There is then another twist: the often exquisite blues, greens and purples of the facial skin fade almost at once, and the brilliant reds, pinks, oranges and yellows of the underparts do so steadily over the months and years, espe-

cially if the specimen is left in daylight for any time. Consequently, museum skins can never convey the full glory of the living creature: trogons, more than any other family of birds, need to be seen alive for the real force of their beauty to strike home. Their red pigment, zooerythrine, is a lipochrome similar to that found in the Scarlet Ibis (*Eudocimus ruber*), the spoonbills (*Platalea*) and the flamingos (Phoenicopteridae), and is dependent for its effect on diet. A yellow-bellied species such as the White-tailed Trogon may acquire red tints on the underparts if it consumes too many carotenoids.

A third trogonid characteristic is the densely barred or vermiculated wingpanel, which is exhibited by all species apart from the genera *Pharomachrus*, *Euptilotis* and *Priotelus*. This panel is formed by the upperwing-coverts, the tertials and the outer webs of the secondaries, and varies among species. In males the pattern is normally white on black, whereas in females it is commonly buff on black. The significance of the wingpanel is not obvious, although it must play a part in species recognition.

The tail is also distinctive, and again appears to play a key role in species recognition. The central feathers are long and broad, and conceal the three outer feathers. The latter are heavily but evenly graduated, so that the outermost is only half the length of the whole tail, and are usually patterned in black and white, producing different types of barred or pied effects, so that a particular "signature" is conveyed by the undertail of a perched bird. When a trogon brakes in flight, these feathers are splayed, momentarily revealing a further dimension of the beauty of these birds.

In the African trogons, the upperparts and breast are green, and the belly is red. The New World species have the upperparts and breast golden-green, blue-green or violet-blue, and the posterior underparts red, orange or yellow; one species, the Surucua Trogon, has a northern race with a yellow belly and a southern one with a red belly, suggesting that the two were once separated and on their way to becoming full species. Females are plainer, being brown, grey or slaty where the males are green, but with the belly coloured nearly as brightly as that of the male. The dominant colours of male Asian trogons produce some dramatic combinations and contrasts. They are red below and bright brown above, with a black head and a white undertail; moreover, a rich blue extends back along the sides of the bill onto the bare fleshy margins of the mouth, and often also around or before the eye, making these birds even more startling than their African and American counterparts, despite their lack of iridescence.



The Surucua Trogon occurs as two distinctive subspecies. That in east-central and northern south-east Brazil has an orange-yellow belly and a yellow orbital ring, whereas these features are respectively red and orange in birds south of those areas. It seems likely that the two races were once separated, perhaps in different habitats, allowing different forms to develop which were in the process of developing into separate species before they came into contact with one another again.

[Left: Trogon *surrucura surrucura*, Cantareiro, São Paulo, Brazil. Photo: Edson Endrigo.

Right: Trogon *surrucura aurantius*, Serra do Alambari, Rio de Janeiro, Brazil. Photo: Luiz Claudio Marigo]



Trogons are arboreal forest birds. Their short, rounded wings allow for a strong, swift flight action, making for great manoeuvrability in limited forest space; over longer distances the flight is undulating, with bursts of rapid wingbeats. Trogons do not usually fly far, however. They normally spend long hours sitting motionless on a favourite perch, only occasionally dropping down to secure a prey item on the ground, where they are handicapped by their weak feet and short legs. Paradoxically, their feet are perhaps the trogons' most interesting feature. It is the first and second toes that point backwards, not the first and fourth as in other zygodactylous birds. This male Collared Trogon shows the outspread wings and feet to advantage as it brakes to enter its nest-hole in a rotting tree trunk.

[Trogon collaris collaris,  
Manu National Park, Peru.  
Photo: Günter Ziesler]



The greens and blues of the upperparts of the American and African species are metallic, with the result that they change dramatically with the angle of the light. Viewed directly from above, an African trogon shifts from bottle-green to, at very narrow angles, a gorgeous royal blue. An American one, a Collared Trogon for instance, can appear coppery-yellow, even reddish in places, but a change of position turns it bottle-green or even a dense green-blue. Observed from below as it perches in the subcanopy, a Resplendent Quetzal, with its long glittering tail adornment, shifts breathtakingly from a coppery-tinged emerald to a rich powdery blue. Four different structures, distributed among five genera, have been identified as producing the iridescence in the plumage of the trogons.

Trogon plumage is notably soft, fluffy, dense and dry-textured. There are ten primaries, which are falcate or subfalcate terminally, the outermost being much the shortest, although the inner primaries and the secondaries are also short. The tail has twelve broad and nearly truncate rectrices. The shafts of some rump feathers are produced as hidden spines, and, of course, the quetzal "tail feathers" are in reality extended and modified uppertail-coverts.

All trogons have a subterminal notch on the culmen, behind the hooked tip, and some species have the edges of the mandibles serrated; this does not appear to have any taxonomic significance, but reflects a feeding adaptation, although the ecological correlates of bill serration in trogons remain undefined. The nostrils and the base of the mandibles are concealed with well-developed, curved, bristle-tipped feathers, the rictal bristles around the bill being reminiscent of such birds as the nightjars. The bill is shorter than the head and is broad basally, so that it appears triangular in vertical profile. The eyes are large, and this would appear to reflect the birds' general niche as subcanopy hunters, operating in relatively dark areas. In some species, the eyelids, which are furnished with eyelashes, are brightly coloured, and those of adults shine phosphorescently in the darkness of the nest-hole. The trogonid tarsus is mostly or, in some cases, entirely feathered, and the anterior toes are fused for approximately the basal half. The feet are generally greyish-blue in colour and rarely visible in the field, but those of *Apalharpactes* are a vivid orange. Trogons have a fragile skeleton, with the skull surprisingly thin, but their flight

and heart muscles are very well developed. Their fresh flesh and viscera have a distinctive odour (see Food and Feeding).

The male Resplendent Quetzal is unmistakable, even without its tail-streamers, because of the laterally compressed, helmet-like crest that extends forwards to cover the base of the bill. The morphology of quetzals seems adapted to enable them to feed on large lauraceous fruits. The gape width at the commissure averaged 2.1 cm in five specimens, but the mandibles have sufficient flexibility that fruits 3-4 mm broader than this can be swallowed. The oesophagus, thick-walled, elastic, and ringed by circular muscles that are presumably important in regurgitation, is some 12 cm in length, but it is not used to store food. There is no crop, but the gizzard is muscular.

Young trogons are altricial and, as already noted, those of the African and some Neotropical species show adult-type feathers on the upperparts, whereas others, including the largest *Trogon* and *Pharomachrus*, possess a distinct, dull, spotty-winged plumage, which is replaced by the iridescent adult dress in an early post-juvenile moult. This difference may be related to the length of the nestling period (see Breeding). The first basic plumage is quickly assumed and, except in some larger species, the young bird then resembles the adult of the respective sex. The undertail of the juvenile, however, may have a pattern quite different from that of adults, and this can cause identification problems, but the rectrices are much more pointed than those of adults. Adult plumage is gained by the second pre-basic moult, at about one year of age. In adults, a full moult appears to occur directly after breeding. Replacement of the primaries, at least in the Asian species, is regular-descendant, and the typical tail moult is sequential. Instances of simultaneous growth of tail feathers appear to represent replacement following accidents.

## Habitat

Although certain species of trogon inhabit dry sparse woodland or bamboo thickets, the members of the Trogonidae are essentially forest birds. They tend to frequent the middle strata and shady interior of forest, occasionally also entering the canopy.



Few bird species of any family have achieved the celebrity status of the Resplendent Quetzal. Sacred to the Mayas and the Aztecs, it has become the national emblem of Guatemala; distinguished citizens receive the Order of the Quetzal, and the bird's image appears throughout the country in every conceivable context, from clothing to banknotes. The origin of this cult is the spectacular nature of the male's plumage, in particular of the narrow elongated uppertail-coverts. These magnificent lengthened plumes form streamers that extend up to 65 cm beyond the tip of the tail, a feature which in the past earned the species the name of "trainbearer". The greater upperwing-coverts are also elongated, projecting beyond the line of the closed wing; and further distinctive features include a short, thick, bristly crest and a rather stubby bright yellow bill. The head and upper breast, the upperparts and the tail-streamers are an intense iridescent emerald-green, appearing blue with the angle of the light, while the belly and undertail-coverts are scarlet, and the undertail is white. All the quetzals are notable for their brilliant plumage, but they are peculiar in lacking one of the main trogonid characteristics, the densely barred or vermiculated wingpanel. Marked sexual dimorphism is a feature of all of them, the females being considerably duller replicas of their mates.

[*Pharomachrus mocinno costaricensis*, Monteverde Cloud Forest Reserve, Costa Rica. Photo: Michael & Patricia Fogden]



Trogons have a distinctive shape that is easily recognized. They are chunky birds with a short neck, a long, graduated tail, and a stout, rather chicken-like bill. The central tail feathers are long and broad, while the outer ones reveal on their undersurface the variously barred patterning that is such a feature of the bird when perched on a horizontal branch with the tail hanging vertically down. The colour of the prominent eyering and the pattern of the undertail are often vital details in clinching the field identification of the species. The loss of a tail feather has upset the symmetry of this Masked Trogon's undertail pattern.

[Trogon  
personatus assimilis,  
Bellavista Reserve,  
Pichincha, Ecuador.  
Photo: Philip Harrison]

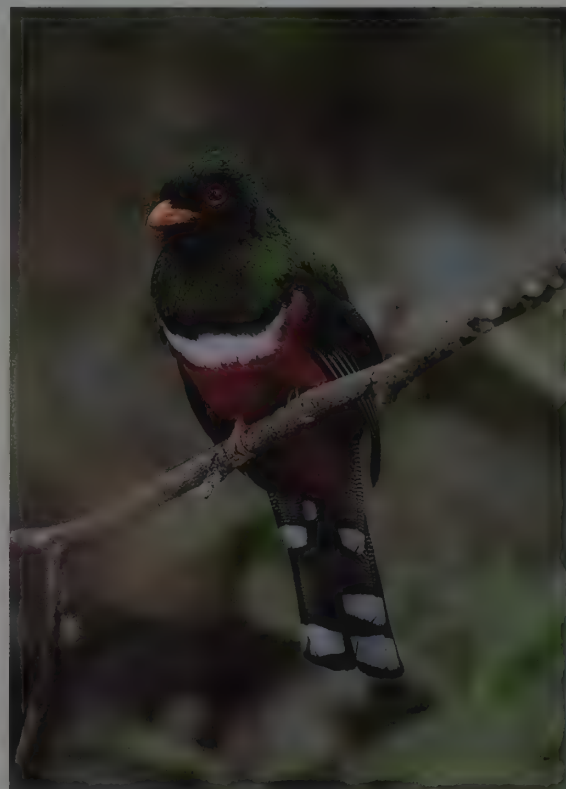
Typically, however, they are to be found perching upright on horizontal branches between the foliage and the trunk. Given the shortness of their legs, horizontal branches are important; furthermore, since most of the large arthropods which many species target live on the undersides of leaves, this mid-storey perching habit presumably abets their visual searching.

In Africa, much the most successful trogonid, the Narina Trogon, has managed to penetrate a wide variety of wooded habitats, ranging from equatorial forest through to fairly open savanna, and from sea-level to over 3000 m. Its two congeners are much more constrained, the Bare-cheeked Trogon (*Apaloderma aequatoriale*) being restricted to Lower Guinean forest and the Bar-tailed Trogon to the montane regions which fringe that forest. There is some competition between them, so that the Bar-tailed tends to replace the Narina Trogon upslope, although the two overlap in some areas such as the Kakamega Forest, in Kenya, and Arusha National Park, in Tanzania. Where the Narina and Bare-cheeked Trogons overlap, the former tends to occupy more open-canopied, disturbed habitats such as storm-struck areas, old villages and overgrown plantations, while the Bare-cheeked remains in primary forest.

No Asian trogon is as tolerant of such broken, drier habitat as the Narina, although the Orange-breasted Trogon (*Harpactes oreskios*) comes closest. All Asian species inhabit tall rainforest, and all appear to prefer primary formations. The higher montane species, Whitehead's (*Harpactes whiteheadi*), Red-headed (*Harpactes erythrocephalus*) and Ward's Trogons, are believed to be the most sensitive to declines in habitat quality. While the other species are commonly recorded in secondary habitats, they do so, however, in reduced numbers. The Greater Sundas represent the centre of species abundance for Asian trogons, with the Malay Peninsula and Sumatra packing in seven species apiece and Borneo harbouring six. In all three areas, as many as five species may be found within a short distance of each other, and certainly four species co-occur in lowland dipterocarp and other formations. In such cases, they are separated ecologically at least in part by foraging height, and presumably in part by food size, given the fact that the birds in question are either "large", being over 32 cm long and with a notably strong, deep bill, or "small", less than 26 cm, with a more normal-sized bill. Thus, the large Red-naped Trogon (*Harpactes kasumba*) keeps to higher levels than the large Diard's Trogon (*Harpactes diardii*), and the small Scarlet-rumped Trogon (*Harpactes duvaucelii*) lives higher up than the small Cinnamon-rumped Trogon (*Harpactes orrhophaeus*), this last species being frequently found in the shrub layer as low as 3-4 m from the ground.

Such "packing" of species is, as usual, exceeded in the Neotropics. Thus, in 1993, H. Sick reported from two to six trogonids in various regions of Brazil. In Rio Grande do Sul there are two, the Black-throated and Surucua Trogons; in Rio de Janeiro's Serra dos Orgãos, those two and the White-tailed, all having yellow underparts; on the upper Xingu four, the Black-tailed, White-tailed, Collared and Blue-crowned; around the Serra do Cachimbo and near Belém at least five, the Black-tailed, White-tailed, Black-throated, Collared and Violaceous; and north of Cachimbo, on the upper Rio Cururu, the number of sympatric species extends to six with the addition of the Pavonine Quetzal (*Pharomachrus pavoninus*). Elsewhere in lowland tropical South and Central America the situation is similar, with five or six species commonly being present in wetter forest formations, and up to seven in, for instance, Tambopata, in Peru. Elevation allows for further complements of species, and the New World has also produced forms which, like Africa's Narina Trogon, can penetrate much drier habitats: in the north the Black-headed and Citreoline Trogons, and in the south the Blue-crowned and Surucua Trogons.

The diversity of species in the three biogeographical zones appears to be related to niche width. The three Afrotropical species are exclusively insectivorous, and are for the most part only very rarely found together. Their insectivory suggests a straightforward inability to exploit fruit, which may be related to exclusion from this source by other families of birds; indeed, the trogons' specialization on apparently poisonous caterpillars may indicate an even tighter constraint on their foraging ability. The fact that they seldom occur together suggests that considerable interspecific competition would exist. The eleven Oriental species are largely



insectivorous, but they also take fruit in moderate quantity; in the Sundas, there is a marked level of sympatry among a core of lowland forms. Of the 25 Neotropical trogonids, all are both insectivorous and frugivorous, but the five quetzals are predominantly frugivorous; the ecological separation of the Crested Quetzal (*Pharomachrus antisianus*) and the Golden-headed Quetzal (*Pharomachrus auriceps*) remains to be clarified. This greater use of fruit allows Neotropical birds to achieve a higher density of species per area, and probably also a greater density of individuals per area. It may well be that the Afrotropical species are the least abundant and the Neotropical ones the most abundant, as a result of this diversification of niches in the New World.

Body mass does not necessarily correlate with abundance. J. Terborgh and colleagues were able to measure the abundance levels of four trogon species in a study plot at Cocha Cashu, in Amazonian Peru, publishing their results in 1990. The heaviest of the four, the Black-tailed Trogon at 122 g, was also the commonest, with 13 pairs per km<sup>2</sup> and a territory size of around 5 ha, whereas the lightest, the Violaceous Trogon at 44 g, was also the least abundant, with just 3.5 pairs per km<sup>2</sup> and a territory size of around 14 ha. The other two, the 59-g Collared and the 61-g Blue-crowned, occurred at densities of 8 and 8.5 pairs per km<sup>2</sup> and occupied territories of 8 ha and 7 ha, respectively. A fifth species, the White-tailed Trogon, was also present in the study area, but at a density too low to measure. Most interestingly, J. V. Remsen and others found that the Black-tailed Trogon differs significantly from the other three quantified species, as well as from the White-tailed, in being markedly more frugivorous, so that a correlation between abundance and dietary habit is clearly suggested. One measure of the home-range sizes of Resplendent Quetzals resulted in an estimate of 6-10 ha, which tends to match this notion: the highly frugivorous quetzal is half to three-quarters as heavy again as the Black-tailed Trogon, yet on this evidence its home range may sometimes be only marginally larger.

## General Habits

Apart from their great beauty, trogons are notorious among biologists and birdwatchers for their lack of other immediately engaging qualities. Their solitary, arboreal, still-hunting behaviour is a

strategy that involves the capture of relatively few, large nutritious items per day. The birds remain still while seeking food, they remain still while digesting it, and the work of food capture takes a matter of seconds. Unsurprisingly, therefore, trogons are characterized as highly sedate, stolid or even sluggish birds which spend the great majority of the day perched motionless and inconspicuously, often in an erect but hunched posture, with the long tail directed almost straight downwards. Generally speaking, their main periods of "activity" are in the early morning and late afternoon, although this is, of course, entirely typical of tropical-forest birds.

Lack of movement is as much an anti-predator strategy as it is a predation strategy. Trogons, like the owls, can turn the head through 180°, and observers on all continents have referred to the "uncanny knack" trogonids have of always orienting the back towards a person and keeping watch over their shoulders, thereby shielding the bright-coloured underparts from view; even a fledgling Narina Trogon has been seen to do this. The broad, truncated tail can look like a strip of bark or dry leaf, camouflaging the bird to a remarkable degree. Observers have also commented, often with depressing lack of charity, on the confiding nature of trogons, the word "stupid" repeatedly figuring in their descriptions. Indeed, many collectors found that the birds would not fly far even if shot at repeatedly. Some species are particularly trusting: in the New World the Collared Trogon is one of the "most unsuspicious", while B. Smythies wrote that in Asia the Orange-breasted "almost forces itself upon the observer's attention and often the native hunter's gun". Clearly, however, the apparent tameness of trogons is an aspect of their innate anti-predator still-perching behaviour, and has nothing to do with intelligence levels.

When a trogon flies, it is almost always for only a short distance. Not least among the reasons for this is that trogons appear to be strongly territorial, and their territories, as noted above (see Habitat), may be very small, so that long flights are largely unnecessary. Only montane species tend to make regular flights over distances of more than a few hundred metres. The action is strong, swift, buoyant and efficient, the bird flitting from one vantage point in the forest to another. Over longer distances the flight is deeply undulating and slightly rocking, with intermittent bursts of rapid wingbeats; in 1964, P. Slud referred evocatively to the Resplendent Quetzal's "headlong bounding flight" and to the Slaty-tailed Trogon's "hurtling dips". In the initial spurt of a foraging sally, the

bird flutters rapidly from side to side like a frightened dove, the pointed primaries and expanded tail twisting sharply, leading to a short rising glide terminated with jerky braking movements, also like a dove's. From anecdotal reports it appears that the flight may be quite noisy, at least during foraging sallies, as has been indicated for Bar-tailed and Orange-breasted Trogons and for both Caribbean species, but also very quiet in other contexts, as reported for Narina and Bar-tailed Trogons and for the Resplendent Quetzal. Indeed, the noiselessness of this last species' flight means that the bird can sometimes take an observer by surprise as, in the words of D. R. Dickey and A. J. van Rossem, it passes through the understorey "like a streak [with] only the slightest suggestion of a wing whisper". Male Resplendent Quetzals take flight by dropping backwards off a perch, apparently as a means of preventing the tail-streamers from soiling and spoiling on the branch through a forward take-off, although the streamerless females also sometimes move off backwards.

Incidentally, although it has been claimed that Resplendent Quetzals never descend below 3-6 m during their lifetime, they occasionally swoop to ground-level shrubs, such as *Rubus*, to take berries. Moreover, they have even been seen landing on the ground in pursuit of lizards or insects, or to defend their nest against squirrels.

When alarmed, Baird's Trogon rhythmically spreads and folds its tail with a rapid movement, sending brief flashes of white to an observer positioned behind. This display is different from that of some other trogons with less white on their rectrices, which may move the tail forwards and upwards. In Asia, the Malabar Trogon (*Harpactes fasciatus*) has the habit, when nervous and preparing to fly, of bending forwards and expanding and flicking up the tail while giving a low mewing twitter. Trogons join in mobbing enemies and potential predators in the same way as do other birds, but generally their mobbing may be rather passive, perhaps of a type intended to attract other, more aggressive mobbers. Elegant Trogons have been seen to use a wing-and-tail flit, flicking the wings and then slowly raising and lowering the tail, accompanied by series of four to ten rapid staccato chucking notes.

There are rather few reports of predation on trogons. A fruit-feeding White-tailed Trogon was seen being caught by a Mantled Hawk (*Leucopternis polionota*), and the feathers of a Collared Trogon have been found in a grove frequented by a White-breasted Hawk (*Accipiter chionogaster*), while a margay (*Felis wiedii*) caught a brooding adult Resplendent Quetzal. It is not clear if the scarcity of reports on predation levels has any significance. In 1926, A. Wetmore reported of the Blue-crowned Trogon that its body "exhales the same strong odor found in cuckoos, particularly in the *Crotophaginae*", and that statement, together with the repeated comments of observers that trogons possess an unpleasant smell, may point to a form of unpalatability which serves to discourage predation. This, in turn, raises the speculation that some species may be less palatable than others, and may consequently be mimicked. Whether it is true that the Bare-cheeked Trogon, when threatened, ejects a malodorous liquid remains to be confirmed, but this report presumably refers to defecation, which seems entirely plausible.

The roosting habits of trogons appear to be virtually undocumented. On the basis of one set of observations on a male Slaty-tailed Trogon by A. F. Skutch, published in 1972, it seems that these birds roost in the open. The individual trogon in question slept nightly at the edge of forest beside an old banana plantation, about 5 m up in a densely foliated branch leaning far out over the clearing. Soon after sunset it would appear in the top of a tall tree above the place where it slept; after resting there for a while, the trogon would fly down to a lower perch and pause there, too. It then dropped abruptly down to the small tree, perching for a few minutes on a rather exposed branch, before moving into the clustered foliage. The time at which it retired was 17:50-18:00 hours. Trogons resting during the daytime have been seen to place their wingtips under the long, rectangular, strongly graduated tail, which hangs vertically or is often inclined forwards.

Feather maintenance by the Trogonidae involves typical avian habits. The birds have been seen to sun themselves on exposed upper branches, where they open the bill, fluff out the breast feathers, turn the back to the light source, spread the wings and fan

*The Scarlet-rumped Trogon, one of the smaller Harpactes species of South-east Asia, displays the bright plumage colours characteristic of the family, the male being predominantly red, brown, black and white. The iridescent sheen of the African and New World genera, however, is completely lacking in this genus. Like its congeners, it exhibits a blue eyering and bill, with the blue on the latter extending to the bare skin around the mouth. The startling blue eyebrow is shared with the very similar Cinnamon-rumped Trogon (Harpactes orrhophaeus), from which it differs in its smaller size and, more noticeably, in its diagnostic scarlet rump.*

[*Harpactes duvaucelii*, Danum Valley, Sabah. Photo: Frank Lambert]





Photo: Joe Tobias]



Singing appears to indicate territorial occupation. Trogons everywhere are very responsive to playback of tape recordings, or at least they are if they themselves are singing. At certain times of the year, in Africa and Asia, the birds are silent, but they very quickly begin singing at the onset of, and sometimes even just before, rain. In the New World, singing seems to occur in some degree throughout the year, although it becomes much more persistent in the breeding season, when it may even be heard on moonlit nights. A whispered version may be a form of subsong. Males do most singing, but on all three continents females also perform, and members of a pair respond to each other at the start of breeding. At this time, the male may move from perch to perch

The Asian *Harpactes* species exhibit a high degree of similarity in their songs. All of them give slight variations of a steadily repeated, hollow, musical and rather ventriloquial "kau" or "klew" note, inflected so as often to sound disyllabic. Some species repeat the call in a series of up to ten or more, while some emit as few as three or four notes per series. Furthermore, some songs are even-pitched while others descend the scale, and some run at an even speed whereas others accelerate. In the other Asian genus, *Apalharpactes*, the Sumatran Trogon's song is markedly different, not just from *Harpactes* but from any trogon song known. The Sumatran species utters a high, whistled, deliberate "wi-wi wheeer-lu", repeated every few seconds. It may be that

within its territory, or occupy a particular songpost for long periods; either way, calling can become almost incessant. The Bar-tailed and Narina Trogons jerk the tail downwards, and sometimes spread it, with each note uttered, and the latter species also inflates the blue gular skin with each note. A singing Violaceous Trogon throws its head back 45°, and a singing Elegant Trogon does so until the head is nearly vertical.

Of course, trogons have other elements in their vocabulary besides singing. The Elegant Trogon has been found to possess five vocalizations. These are: (1) the main song, given by both sexes, consisting of three to eleven "coa" notes, delivered in the breeding period from March to August; (2) a similar series of "co" notes, used in courtship by both sexes; (3) a rapid "coacoacoaco", given by both sexes outside the breeding period, from September to February; (4) an even faster "cocococococo", given by males in dispute; and (5) a hoarse "criccickkk" in alarm. It may well be that most *Trogon* species have similar vocabularies; certainly, the alarm call of many has been written as a sharp chattering "krrrrr" or "turrrr", or suchlike, which matches (5) above. Various other clucks and squawks have been mentioned, and the quetzals appear to have an interesting set of extra calls, including a loud self-advertising call given in display-flight during the breeding season.

An apparent mating "duet" has been recorded from Bar-tailed Trogons. In this, one bird repeatedly jumped backwards and forwards over the other as it sat crosswise on a branch, before the two drew a little apart; thereupon one uttered a sequence of high-pitched notes, which the other also gave immediately after the first bird's fourth note.

Sick referred to a peculiar vocalization of certain *Trogon* nestlings that is different from the croaking which they emit when receiving food. This unusual utterance consists of an ascending, accelerated sequence similar to the adult's song, and it is persistently repeated at short intervals.

## Food and Feeding

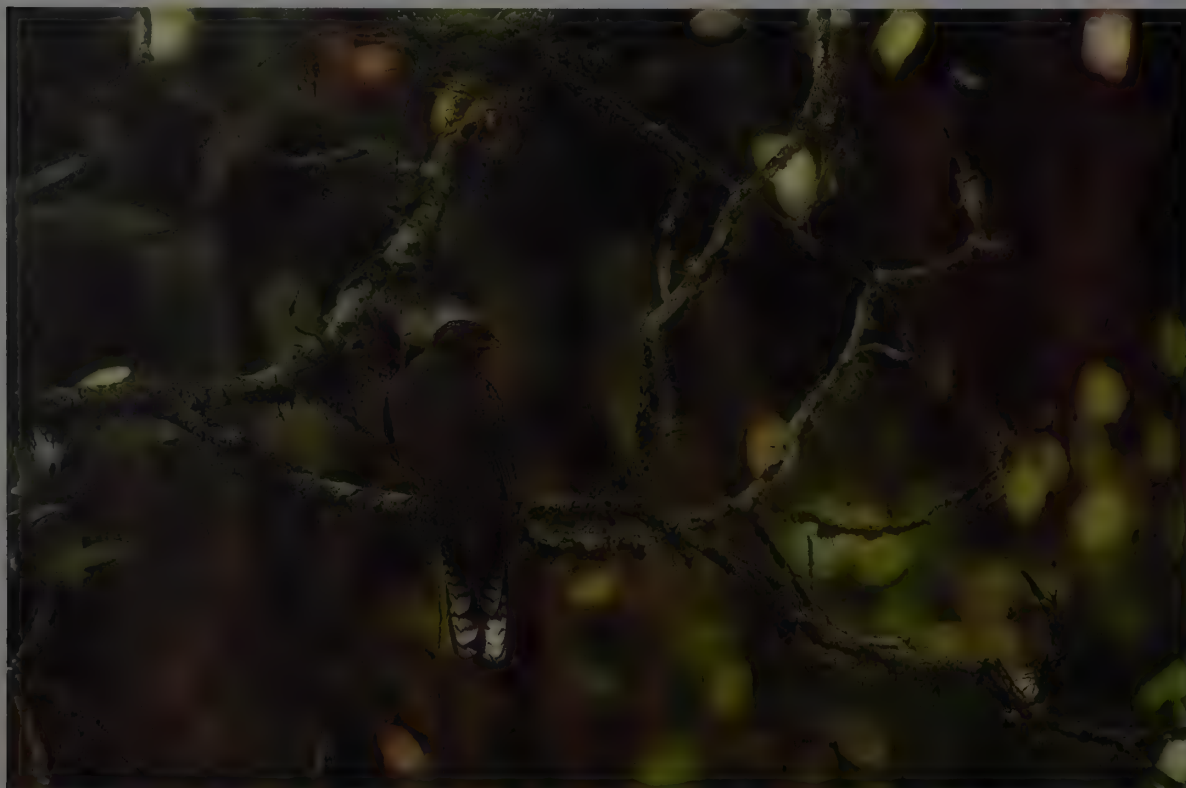
Trogons belong to a guild known as "sallying substrate-gleaners". This is an accurate enough description for these birds, except that the word "gleaner" tends to connote insectivory (*sensu lato*) only, whereas the short sallying flights of trogons are also made to col-

lect fruits and, occasionally, small vertebrates. In fact, their diets vary regionally and taxonomically. The African species are exclusively insectivorous or carnivorous, while the Asian ones consume a mixture of animals and fruit, the former apparently predominating. The diets of the New World trogons are similar to those of the Asian ones, but their animal and fruit food is taken in significantly variable proportions, culminating in the quetzals, which are, for most of the year, almost entirely frugivorous. To some extent, frugivory is correlated with body size. At least in the Neotropics, the larger trogons as well as the quetzals are predominantly frugivorous, while the smaller species tend to take greater proportions of arthropods; it seems quite likely that a similar situation will be found to apply among *Harpactes* species in Asia.

The foraging flight is of three main types. The most commonly used, since it involves both animal and vegetable food, is a short rapid sally to a fixed target. The bird then either briefly hovers, as is the case with the smaller species, or momentarily stalls, as do the larger species, to pick an animal off a leaf, stem or bark surface or to pluck a fruit from the outer surface of a bush or tree. The Slaty-tailed Trogon's relatively narrow wing has prominent, deep square slots which allow it to slow sharply in its final stalling rise to the food source, and the broadly spread tail helps to control the precise moment of the stall. Collared Trogons seen with many other birds at a small fruiting tree never perched in it, but, confining their attention to the top of the tree, they approached from neighbouring trees in a low silent glide and upward swoop; in this way, each one came up to the fruit from below, hovering a moment with a loud fluttering of wings to snip berries from the cluster, and apparently swallowed these while on the wing.

The other two types of foraging flight involve only animal prey. One is a jinking pursuit of a flying insect, snatched with no less agility and precision than a drongo (*Dicrurus*) or flycatcher (Muscicapidae). These flights are usually conducted in forest-edge contexts, and by the smaller species: the Scarlet-rumped Trogon has been seen several times sallying out over scrub like a shrike (*Lanius*). The other type is a pouncing attack on an animal, the trogon landing briefly to snatch up the prey and carry it to a perch for consumption. Lizards and frogs are the commonest of the occasional vertebrate victims of these attacks.

These are not, however, the only foraging techniques used by these birds. Collectors have quite frequently reported insect



With one exception, the quetzals are montane species. The White-tipped Quetzal is restricted to small areas of Colombia and Venezuela, ranging up to 2500 m in the former and occurring at somewhat lower altitudes in the latter. It frequents the middle and upper levels of humid forest, and also tolerates forest edge, clearings, secondary growth and even, at times, wooded ravines amid coffee plantations. As its diet is thought to consist solely of fruits and berries, it is unlikely to have to compete with other trogon species in its range, which are mainly insectivorous. The female White-tipped Quetzal, a drabber version of the male, is shown here, splendidly camouflaged on a leafy perch.

[*Pharomachrus fulgidus fulgidus*, Venezuela.  
Photo: Roland Seitre/Bios]



eggs in trogon stomachs, and have sometimes explained this as the result of the bird's having consumed a pregnant adult insect. Nevertheless, a single report of a Narina Trogon describes a kind of behaviour that must occur in many species, namely that "when in search of the beetles and larvae which constitute its diet it creeps, rather than hops, about the branches..."; it seems very likely that such behaviour leads to the discovery of insect eggs and pupae. The finding of the wings of a nestling bird in the stomach of a Collared Trogon suggests that, on rare occasions, nest predation may also result from this kind of shuffling search. Resplendent Quetzals very occasionally take fruit from a perch, this having been recorded as 2% of observations in one study.

The chief animal victims of the first aerial foraging technique, termed "hover-gleaning", are large caterpillars, both smooth and hairy, and large arthropods such as cicadas, moths and beetles. Sometimes it is the leaf on which a caterpillar sits that is snatched, the former being dropped as the bird swallows its meal, although leaves in the stomachs of shot birds, both in Asia and America, may have been ingested along with the sitting insect. A Red-headed Trogon has been seen catching cicadas against the trunks of trees. The persistence of activity into late twilight of both this and the Malabar Trogon may be related to the exploitation of certain insects, such as cicadas and moths, that become active at dusk. Large arthropods are beaten against a perch, first on one side, then on the other, the trogon throwing its whole body into each blow. In addition, however, the bird uses its powerful bill to scrunch hard insects; the severity of a bite once given to a field assistant when retrieving a wounded Collared Trogon was unwelcome proof of just how powerful the trogonid bill is.

Trogons, like cuckoos, appear to favour caterpillars, including the noxious forms, although, except perhaps in Africa, they do not specialize on them. It may well be that the malodorous nature of the trogons' excrement, nests and flesh, noted by various authors, is related to this particular dietary niche, as it clearly is in the cuckoos. The beating of captured insects, when the bill is otherwise so capable of their rapid dispatch, may well be part of the process of ridding these prey of their poisonous contents.

In Asia and the Americas, trogons often join mixed-species feeding flocks, seeking insects and other animals flushed as the bird wave passes through their territories. At Tambopata, in Peru,

all seven trogonid species, including the Pavonine Quetzal, are listed as joining such flocks, the quetzal presumably temporarily abandoning frugivory when it does so. In Asia, it has been noted that trogons, like the malkohas (*Phaenicophaeus*), take up trailing positions 30-300 m from the noisy front wave. As V. Legge nicely observed as long ago as 1880, "lastly, at a little distance from the sociable gathering, sits aloof a solitary Trogon, as if it had come to see what was the matter, but scorned to associate with its lively neighbours". A more recent observer noted, however, that the trogons would fly into the flock, remain still while the flock moved on, and then, after a time, fly to catch up with it once more. Much more rarely, trogons have been recorded following monkey troops, and Black-throated Trogons, like most avian insectivores of lowland forest, occasionally take advantage of the activity of army ants.

There may be a correlation between diet type and foraging station. The food taken by Elegant Trogons in El Salvador appeared to consist of proportionately more animal matter than did that of the country's four other trogons, all of which forage at a higher level. As already noted (see Habitat), the larger-bodied Neotropical trogons tend to be more frugivorous than the smaller-bodied birds, and this seems very likely to be mirrored in the Old World, where Orange-breasted and Cinnamon-rumped Trogons appear to feed more frequently on the ground than do their larger, high-foraging congeners.

A correlation may also exist between diet type and foraging pattern. Insectivorous trogons may be relatively territorial all year around, whereas the more frugivorous species may travel in small, loose groups in search of fruiting sources. The pattern of foraging by Citreoline Trogons observed at fruiting trees in spring certainly suggested that the birds were turning up in such groups, and similar behaviour has been seen in Resplendent Quetzals and, outside the breeding season, Eared Quetzals. Clearly, it is normal for several trogons to be present in a fruiting tree, even if these birds are solitary or in pairs at other times. Although intraspecific competition is apparently undocumented, interspecific rivalry has been reported at least once, when an Elegant Trogon was noted driving Eared Quetzals away from food trees. Indeed, competition from both the former species and the Mountain Trogon may have contributed in part to the Eared Quetzal's localized distribution in Mexico.

A small, dapper South American trogon with a prominent orange orbital ring, the Blue-crowned Trogon is not confined to pure forest. In addition to occupying várzea, riverine forest and tall secondary growth, it can be found in much drier savanna woodland, dry semi-deciduous forest, lake margins, forest clearings, and woodland edges; in Brazil, it has been recorded from palm swamp and surrounding dry scrub and caatinga. It reaches quite high elevations in the south of its range, being common in montane woodland at up to 1500 m in Argentina, and ranging even higher in Bolivia. The well-defined white breastline of the nominate race is faint or absent in the subspecies *peruvianus*.

[Trogon  
*curucui peruvianus*,  
Tambopata Reserve, Peru.  
Photo: Günter Ziesler]



Vegetarianism among trogons takes various forms. Although it may be usual for the birds to target fruits and berries which they can seize whole in the bill, they also bite pieces out of larger forms. Thus, Elegant and Citreoline Trogons take the flesh off *Pithecollobium dulce* fruits and discard the seeds before ingestion. A Violaceous Trogon has been seen tearing pieces from dangling fruiting spikes of *Cecropia* trees, carrying each larger fragment to a perch before swallowing it, while a Surucua Trogon was watched apparently feeding on the bark of a dead cactus, although lichen and aphids were also present. As already noted, leaves have occasionally been found in trogon stomachs; in addition, that of a Whitehead's Trogon was found to contain some stones, which suggests deliberate ingestion to assist with the processing of green matter. Perhaps the most interesting case concerns the Cuban Trogon, which often feeds at or on flowers: this species has the tongue split at the tip, apparently to facilitate the capture of pollen or nectar, unless, conceivably, it is designed to assist in the taking of small animals inside the flowers.

The Slaty-tailed Trogon and the Resplendent Quetzal share much the same diet, but differences in the size and strength of the bill affect the ways in which the two species handle fruits. The Slaty-tailed's bill is narrower, deeper and heavier than the quetzal's, even though the bird itself is markedly smaller; the trogon eats piecemeal, while the quetzal swallows fruit whole. Both, however, are compelled by competition from other frugivores, notably toucans, to select fruit carefully on the basis of quality. In aviary experiments, Slaty-tailed Trogons showed an almost exclusive preference for certain ripe fruit, whereas a toucan took different fruits in various stages of ripeness; trogons would thus be expected to take fewer fruit species in their diets. Similarly, while toucanets can move about in the branches and take fruit of any quality, the greater energetic costs incurred by the quetzal in sallying to the lower outer areas of a tree, where rivals seem least comfortable, mean that it must select fruits with a high energy yield. Consequently, in one study, toucanets fed on 83 species of fruit, whereas Resplendent Quetzals took only 43.

The frugivorous behaviour of Neotropical trogons makes them the most important family, along with the cotingas (Cotingidae) and the toucans, for the dispersal of the seeds of large fleshy fruits. In Panama, the Slaty-tailed Trogon has been

shown to be an important disperser, by regurgitation, of the fruits of *Virola surinamensis*, accounting for 11% of all fruits dispersed. All quetzal species are likely to be equally important. Although it has been suggested that Resplendent Quetzals are poor seed-dispersers, since 60-90% of all seeds which they drop fall directly beneath the parent tree or within 100 m of it, it is probable that the sheer quantity of seeds taken by the species results in a sufficient number being more widely dispersed.

A good example comes from Monteverde, in Costa Rica. Although the Lauraceae constitute only 4% of bird-dispersed tree species at Monteverde, they comprise almost 50% of the fruit species consumed by Resplendent Quetzals, and total 80% of the seeds regurgitated during the breeding season. The Lauraceae provide large seeds coated with a nutritious pericarp, and it is evident that the quetzals are specialized to live off these fruits throughout the year. When the birds move out of Monteverde after breeding, they effectively "track" the phenology of lauraceous fruits over the non-breeding season. The peak breeding period, in April and May, is closely correlated with peak production, in terms of greatest abundance and species diversity, of lauraceous fruit.

Young trogons are fed mostly on insects. The parents do not appear to make much allowance for chick size, and Black-throated Trogons feed such large prey to their young that the intervals between nest visits are unusually long, although sometimes the prey is simply too large for the chicks to take. In 1972, Skutch observed that a male Baird's Trogon seemed to do most of its hunting in the high treetops, since its approach to the nest was always from above; many green insects were brought in, perhaps because such animals are particularly nutritious, this fact also suggesting that much foraging was done among fresh green leaves.

Among the Trogonidae, the best-studied nestling diet is that of the Resplendent Quetzal. Even in this frugivore the young are fed predominantly on animal food, at least up to the tenth day, although a little fruit may be given from day two. On hatching, the young quetzal already has an enormous mouth, which at ten days is as large as or even larger than that of the parents; at this stage, the food items given to the chicks are no different in size from those taken by adults. On one occasion, a male chick was witnessed eating, over the course of 30 minutes, a wild plum, an



The colourfully plumaged Red-headed Trogon, with its diagnostic dull crimson head and underparts, is chiefly a mountain species. Its marked preference for primary forest is shared by the other Asian trogons, most of which will also tolerate secondary growth, although they are found in smaller numbers there. By contrast, the Red-headed is a denizen of deep forest interiors, and is considered very sensitive to any deterioration in the quality of its habitat. It lives in dense broadleaf, evergreen and mixed bamboo forest up to a maximum altitude of 2000 m. It favours the middle storey and low canopy, where it feeds on insects and other arthropods, as well as bamboo leaves and berries.

[*Harpactes erythrocephalus chaseni*, Fraser's Hill, Peninsular Malaysia. Photo: Morten Strange]



A small species with attractive colours, the Black-throated Trogon is a lowland bird, seldom found above 1000 m. It occupies the lower and middle storeys of moist primary forest and nearby secondary growth, at times frequenting cocoa plantations, more open woodland, and edges and clearings with a dense understorey. It is very sensitive to logging, with a marked tendency to disappear from disturbed areas. Remarkable in this photograph are the protruding short outer tail feathers, rarely seen on a trogon perched with its back to the observer. Despite its colourful plumage, the bird is inconspicuous, especially while it remains motionless.

[*Trogon rufus chrysochlorus*, Iguazú National Park, Argentina.  
Photo: José & Adriana Calo]



avocado 5 cm long, three more wild plums, a scarab beetle and another 5-cm avocado. The chick's belly becomes grotesquely protuberant, and the skin is so thin that chitinous material can clearly be seen in the intestines. Insects of many kinds, but often including many bright beetles, are fed to the chicks, along with small frogs, lizards and land snails.

Virtually no information is available on drinking by the members of this family. There is a single observation of an Elegant Trogon: it landed on a broken palm and took rainwater from the stump in the typical avian manner, dipping its bill and then raising its head high to swallow. Resplendent Quetzals are believed to obtain water either from their food or from pockets held in epiphytic vegetation.

## Breeding

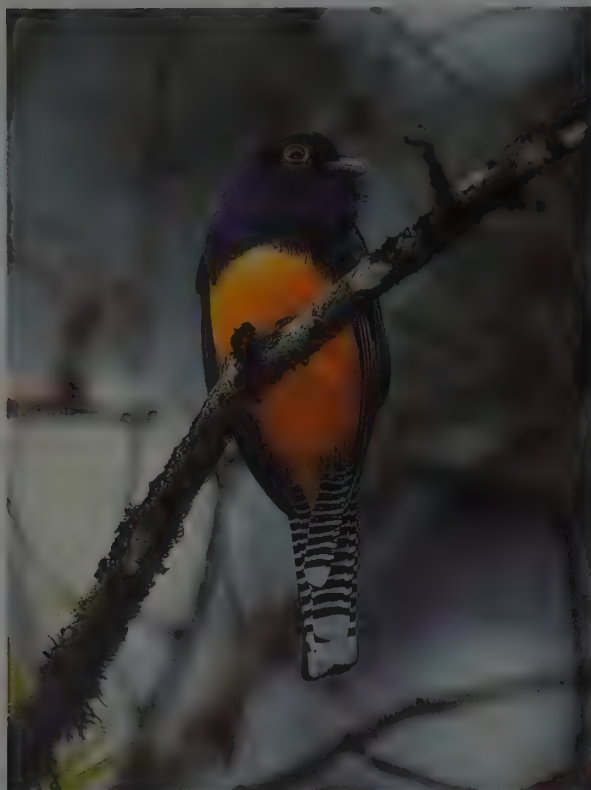
Male trogons show their strong territoriality by the speed with which they react to the playback of their songs, and they confront conspecific intruders of both sexes. Most recorded aggression, however, is related less to defence of a territory as a general food-resource area than it is to the prevention of interference with breeding. Narina Trogons will pursue hole-nesting birds such as Green Woodhoopoes (*Phoeniculus purpureus*) and Black-bellied Glossy-starlings (*Lamprolornis coruscus*), and potential brood parasites such as African and Red-chested Cuckoos (*Cuculus gularis* and *C. solitarius*), although it is possible that the last two are pursued as food competitors. They will also chase away nest predators such as squirrels (*Paraxerus ochraceus*), making a direct flight at the intruder with a snarling or swearing call. Hartlaub's Turacos (*Tauraco hartlaubi*) have also been recorded being chased, but, since they are frugivores that build stick nests, the reasons for this are not obvious. In the case of Bare-cheeked Trogons, even the young help to defend the territory. In the Amazon, Pavonine Quetzals have been seen attacking Black-banded Woodcreepers (*Dendrocolaptes picumnus*) near an evident nest-hole, and Elegant Trogons customarily pursue squirrels, tyrant-flycatchers (Tyrannidae) and flickers (*Colaptes*).

An unexplained phenomenon exists among some territorial monogamous bird species in which males display in noisy groups

of usually up to ten birds, and occasionally as many as 20, often attended by several females. In Africa, wattle-eyes (*Platysteira*) do this, their gatherings being called "parliaments". The behaviour also occurs among trogons on all three continents in which they are found. In the Old World it has been recorded for the Narina, Bare-cheeked and Scarlet-rumped Trogons, and in the New for the Black-headed, Citreoline, Collared, White-tailed, White-eyed, Slaty-tailed, Black-tailed and Hispaniolan Trogons, as well as the Resplendent Quetzal. There have been a couple of occasions when such gatherings were noted to be composed of two species, the Narina and Bare-cheeked in Gabon, and the Collared and White-tailed in French Guiana. The birds sing and follow each other slowly through the understorey, chasing but not striking one another, with leapfrog displacements of the leader. Such assemblages may continue daily for a fortnight, forming early in the day and lasting one or two hours, before each male returns to its own territory. A group of Bare-cheeked Trogons has been seen moving through the territory of another pair when the latter had young, yet provoking no aggression from the resident male, which did not join the assembly. In one instance, a group-calling male Narina Trogon attracted several females, which made short flights from branch to branch near the male; twice a female pointed her bill upwards and gaped wide, with wings drooping, and with the red feathers of one side of the breast fluffed out towards the male, in an apparent attitude of solicitation, but no copulation ensued.

Despite such behaviour, these groups are not leks as normally defined by biologists, because trogons are monogamous and share parental duties; nor are they always formed by bachelor males seeking mates or territories, since the participants return to their individual territories where the female has remained behind. Sometimes, however, it does appear that the majority of participants are unpaired males: Resplendent Quetzals appear to use these assemblies to find a mate, groups of as many as twelve males noisily pursuing a single female, flying from branch to branch.

In the absence of a full explanation for this phenomenon, it is worth noting the findings of one study made in El Salvador. There, the three common trogonids, namely the Violaceous, Black-headed and Elegant Trogons, all appeared to exhibit a genuine bias in sex ratio towards males; even young birds, when



collected, more usually proved to be male rather than female. Moreover, in Brazil, Sick reported a preponderance of males from clutches of four eggs. Whether all species show a skewed sex ratio, and whether there may be a link to trogon "proto-lek" behaviour, are matters for future researchers to investigate.

Existing knowledge of pair formation and pair-bond persistence in trogons is rudimentary. With many species, however, it appears that pair-members maintain a loose association and re-mate in the following season. Behaviour associated with pairing may, therefore, diminish with the duration of the pair-bond, and the types of behaviour involved are certainly very

poorly documented. In Costa Rica, for example, some Resplendent Quetzals return from the Atlantic slope in December already paired, leaving others, perhaps young or widowed birds, to engage in courtship-flights which carry on into May. The primary step for any male trogon, however, is to establish and advertise a territory, by singing. Resplendent Quetzals appear to be the only trogonid known to go further than this, indulging in a remarkable display-flight. The male flies straight up out of the forest, its tail streaming behind, giving a loud, raucous "waka waka waka!", and then dives, wings closed tight, to disappear back into the forest, usually but not always near the initial take-off point. This display is repeated several times a day throughout the spring and summer, with three peaks in the performances, at around 06:00, 12:00 and 17:00 hours; on average, a male performs 0.5 display-flights per hour through the day. As males with long tail feathers make relatively more display-flights than do those with shorter ones, these flights are judged to be aggressive signals to other males, and demonstrate the fitness of the singer by showing the size of its tail. On this basis, it may be assumed that no such displays exist among the shorter-tailed quetzals of South America.

Critical to each year's breeding cycle is the finding and preparation of a suitable nest-site. All trogons are cavity-nesters, using chiefly either decayed stumps and trunks of trees or holes in the nests of social insects. Some species occasionally excavate cacti and tree-fern trunks or use "holes" in the roots of epiphytes, and there is one record, now rather questionable, of an Elegant Trogon's nest in an earth bank. Deciding on an appropriate site is a major challenge for the species which nest in timber. They often have great difficulty in finding a dead tree that is neither too hard for them to carve nor so decrepit that it will not hold the chamber. Sometimes they try again and again until, eventually, they find wood of just the proper firmness. A pair of Baird's Trogons was recorded starting six separate holes in a massive buttressed stump, but completed none of them because the wood was too rotten. Likewise, a pair of Resplendent Quetzals excavated at least five holes in one month, all within 100 m of the nest finally chosen. Trees rot downwards, so the quetzals sometimes excavate nests progressively lower in the tree each year; nevertheless, the density of suitable nesting trees far exceeds the density of nesting quetzals. Wood of the right consistency for

Trogon vocalizations, often loud and resonant, are structurally simple and repetitive, consisting of a series of monosyllabic hooted or whistled notes. Only the quetzals aspire to slightly longer, more complex utterances. All species in the Neotropical genus *Trogon* produce "kyu" calls and, even though the notes vary in speed, number and pitch, specific identification by voice is rather tricky. A typical example, the *Violaceous Trogon*, utters a long series of hollow whistled notes, throwing its head well back as it sings. Trogons are heard much more frequently than they are seen; locating a singing bird in a forest habitat is not helped by the somewhat ventriloquial nature of the voice.

[*Trogon violaceus violaceus*, Arima Valley, Trinidad. Photos: Art Wolfe]



The shortness of a trogon's legs limits arboreal movement, so that the bird invariably chooses a perch on a middle-storey horizontal branch that provides an ideal vantage point from which to still-hunt. On spotting a food item, the trogon most often uses a technique known as sally-gleaning: the target is reached by a rapid sally, and the bird then hovers, or briefly stalls in flight, without alighting, to snatch a fruit from the outer part of a tree or bush or to pluck an insect off the surface of a leaf or trunk. The Citreoline Trogon eats both fruit and insects, in proportions fluctuating according to availability.

[*Trogon citreolus citreolus*, San Blas, Mexico. Photo: Don Roberson]



Whereas only three trogon species occur in the whole of Africa, all of which are insectivorous, the number in the Neotropics is twenty-five, a figure reflecting the higher diversification of the Neotropical species, which are able to exploit both fruit and insect food resources.

The five *Pharomachrus* quetzals are to a large extent fruit-eaters. The Resplendent Quetzal is noted for its partiality to the fruits of the Lauraceae, especially *Ocotea* species,

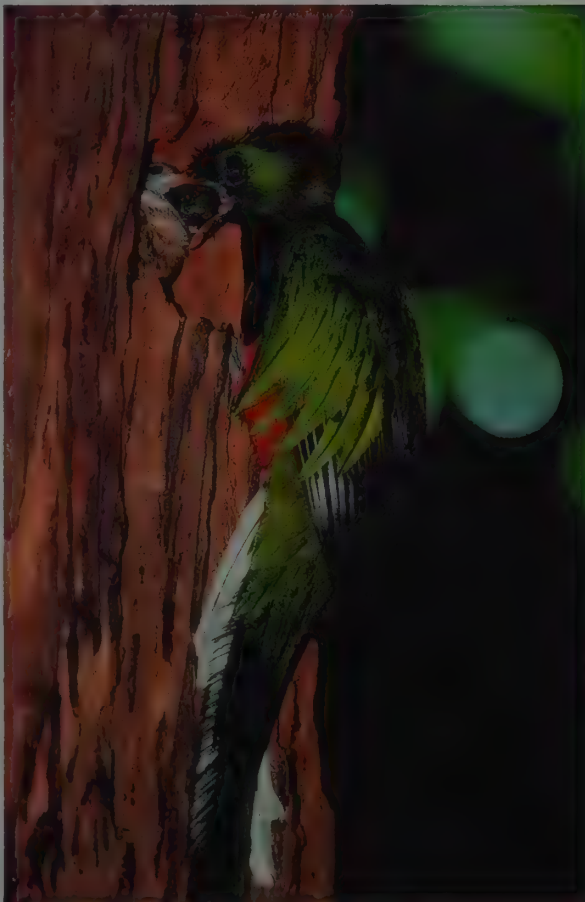
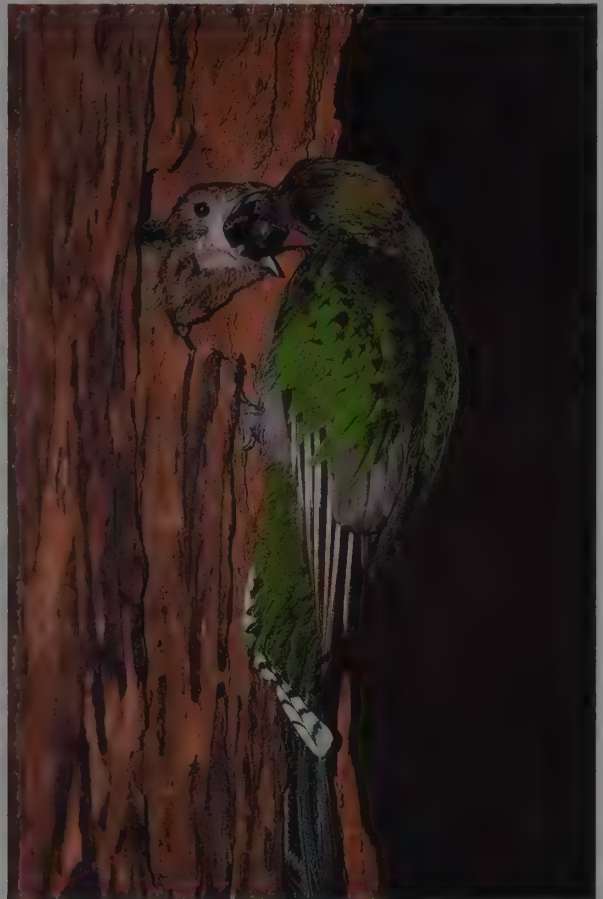
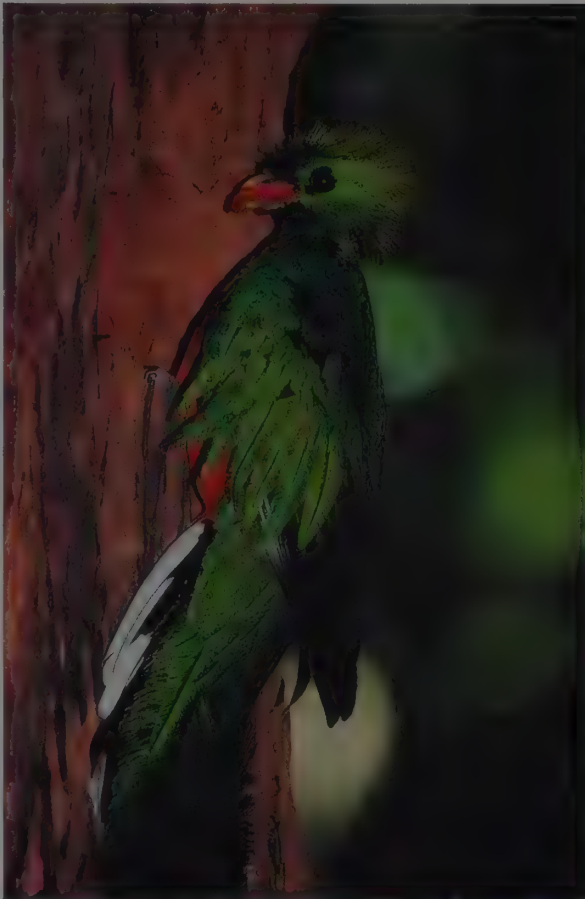
wild relatives of the avocado; these fruits are swallowed whole, only the large seed being regurgitated. It will also take arboreal snails, insects and other arthropods, and small frogs and lizards. Newly hatched trogonid chicks are generally given a mainly insect diet, the parents often bringing very large prey items, regardless of the chicks' size. Even the normally

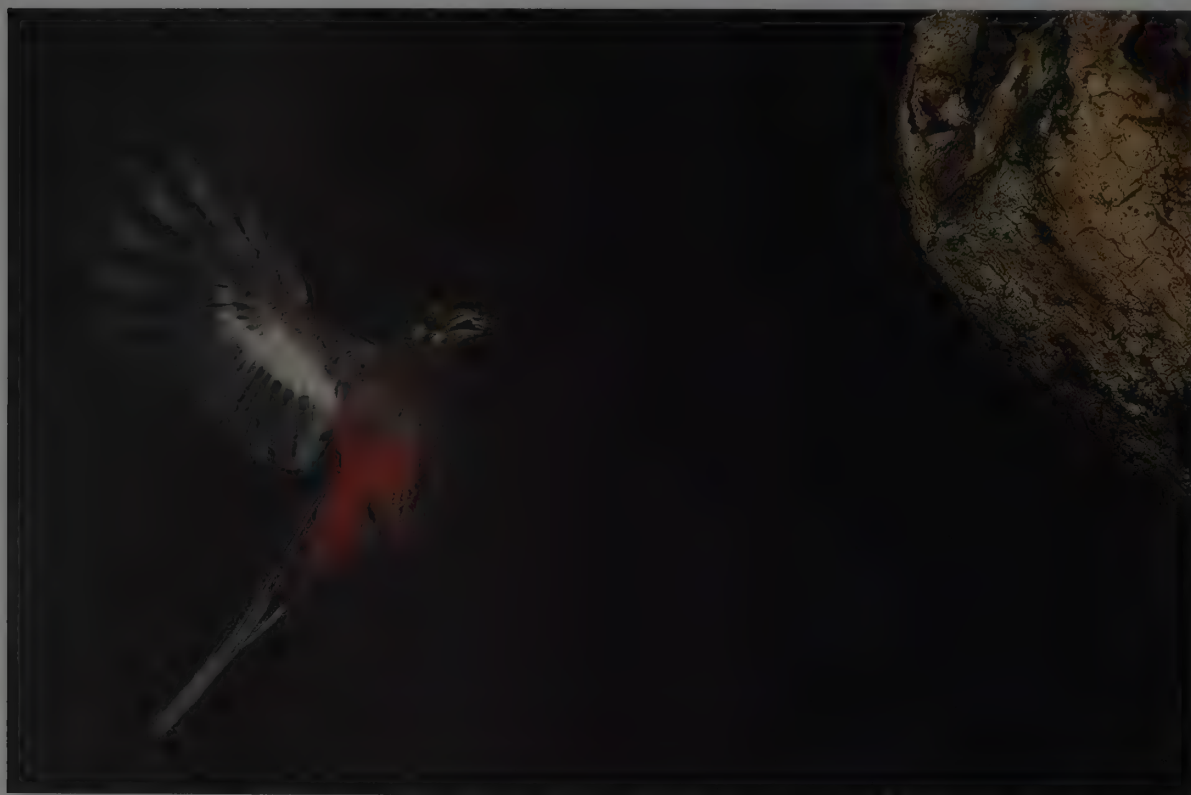
more frugivorous Resplendent Quetzals provide their young with a predominantly animal diet for the first ten days or so. The nestlings seen here appear older and, correspondingly, the food offered comprises more fruit: a thimbleberry, a wild avocado and *Beilschmiedia* fruit, and a small lizard, three fruits to one animal item.

A remarkable feature is the huge size of the chick's gape, which looks as large as the adult's and capable of swallowing a whole avocado; even more remarkably, its gastric juices must be capable of digesting it. Both parents collaborate in feeding their offspring, the male making the major contribution.

The female, with a crestless bronze-green head and considerably less elongated wing-coverts and uppertail-coverts, is not quite as spectacular as her mate, though still quite splendid.

[*Pharomachrus mocinno costaricensis*, Monteverde Cloud Forest Reserve, Costa Rica. Photos: Michael & Patricia Fogden]





Like the two other African trogons, the Narina Trogon is largely an insectivore. It shows a liking for smooth-skinned caterpillars, but rarely takes hairy ones. Its food also includes all kinds of beetles, bugs, adult butterflies and moths, and stick-insects, supplemented with the occasional lizard or frog. This is the most successful of the African trogons, as it is able to tolerate much more disturbed habitat than can its congeners. Although widespread over most of the forested regions of sub-Saharan Africa, and even present at high altitude in one part of its range and in well-wooded suburban gardens in another, it is, nevertheless, uncommon.

[*Apaloderma narina narina*, George, Cape Province, South Africa. Photo: J. J. Brooks]

trogons can be dug into by human fingernails, but it does not crumble to powder when rubbed between the fingers.

A male Malabar Trogon has been witnessed landing on a decaying tree trunk and slapping its tail repeatedly against it. This may well be related to the curious behaviour reported in 1999 by Skutch, who watched a pair of Slaty-tailed Trogons apparently prospecting a rusted piece of vertical sheet metal guarding a chicken run: the male repeatedly flew up and struck the sheet with a loud metallic bang, the female following suit, and both of them kept up this behaviour intermittently for two days. In both cases, the birds were possibly testing apparently suitable nest-sites for resonance, which would indicate their potential for excavation.

It may be that unmated male trogons excavate sites as part of the mate-attraction process, and that a female assesses the site as part of the process of assessing the male. If the female dislikes the site, she leaves it and, perhaps, also leaves the male. A male Elegant Trogon will call persistently in the immediate vicinity of a nesting cavity, waiting for a female to enter the area. He then perches at the entrance and/or enters it, calling constantly, until a female pairs up with him. In this species, which nests in dead trees, only the male excavates, but this is apparently unusual, as many other species which nest in dead wood share excavation duties between the sexes. As the male chews away, small showers of wood particles drift down, and after a session of such work the bird will sit nearby and rid its mouth of sawdust by opening and shutting its bill several times. The name "trogon", incidentally, stems from the Greek word for "gnawer".

Excavation of nests in wood may proceed over several months, and the length of time taken is not necessarily a guide to breeding condition. For species that breed in nests of social insects the action has to be concerted, and both sexes participate. The insect nests are almost always termitaria, and almost invariably active ones, as the structure needs to be sound. The trogons probably eat the termites on the way in, but the termites keep trying to mend the damage to their nest, so the trogons' work has to proceed rapidly. Nevertheless, neither member of the pair will work on cavity creation or improvement unless the other is present to act as sentinel. Even when sometimes digging separate holes in the same termitarium or vespiary, they do not do so simultaneously. When the cavity is completed, the termites appear to seal its internal walls;

after the young trogons have fledged, the insects take back, and presumably refill, the cavity and reseal the entrance. The termitaria used by Black-tailed Trogons in Peru are situated rather low, at an average height of 6-1 m. and are large, with a mean volume of 63 litres; the tunnels excavated by the birds average 7.3 cm in diameter and 19 cm in length, and slope up at 56°, while the nest-chambers average 18 cm in diameter and 15 cm in height. They are not used in subsequent years. Termitaria used by Black-headed Trogons may be positioned so low down, on a fence post for example, that the birds have to land on the ground before flipping up to continue the work of excavation.

The Violaceous Trogon is apparently the only member of the family to utilize wasp nests, and a single record of a pair excavating an arboreal ant nest appears to be the only documented instance of any bird species in the New World using such a nest for breeding. The trogons first eliminate the owners by perching near the nest and either capturing them on the wing or gleaning them from the nest surface, mainly in the cool early morning while the insects are least active. They then hollow out a chamber among the brood-combs at the heart of the nest, presumably eating the larvae in the process. In one case, the birds had to hover and bite pieces out of the smooth surface of the vespiary in order to use the holes as footholds.

Cavities may be of two types. The White-tailed, Baird's, Slaty-tailed, Citreoline and certain other trogons excavate upward-slanting entrance tubes to fully enclosed chambers. Many other species, including the Black-throated, Collared and Mountain Trogons and the quetzals, as well as apparently most, if not all, Asian trogonids, construct shallower, more open niches. In the former case, the parent is totally concealed; in the latter, much of the incubating parent, especially the head and tail, is visible from the front. Unsurprisingly, trogons that excavate termite nests will also carve chambers of the same form in massive dead trunks, while species that nest in open niches are not known ever to occupy termitaria.

When a male Narina Trogon has located a suitable nest-hole, he pursues a female with a slow, gentle, undulating, butterfly-type flight, at each stroke raising his wings almost to the vertical, exposing their white undersurface. He calls repeatedly, fluffing out his breast and belly feathers while flicking his tail up and down, or fanning it widely to expose the white outer rectrices;



the throat patch gleams a metallic blue-green. Such courtship may continue for several days, during which time the pair inspects the nest-site repeatedly. In another observation of courtship, one Bartailed Trogon jumped backwards and forwards over another perched on a bough; the two drew apart and began what seemed to be a mating "song" (see Voice); a third bird sat motionless nearby.

An apparently courting male Slaty-tailed Trogon repeatedly raised his tail while giving a jerky bow or dove-like nod, displaying the red crissum and fluffed green rump and uppertail-coverts. The female also raised her tail and, holding it so for a moment or two, exposed her fluffed red crissum, but she did not nod, and neither sex spread the tail. The two drew near to each other and, keeping their backs turned, continually raised and lowered the tail while uttering a churring chuckle. The closely related Lattice-tailed Trogon has a similar ritual, but, significantly, the normally concealed latticed outer tail feathers are spread outwards from the rest of the tail and are folded to overlap the green middle rectrices.

Narina Trogons copulate frequently until the clutch is complete. In one instance, a female perched on a bare, sunlit branch and the male flew 10 m to her in a slow moth-like fluttering flight, showing a blaze of fluffed red breast feathers; he landed directly on her back, and his tail worked from side to side as he copulated, wings fluttering. In the Elegant Trogon, copulation takes the form of the male flying initially to within 3-5 m of the female, giving the "cocococo..." courtship song, and then flying directly to her, hovering above her for two seconds, taking her nape in his bill, and landing on her back while she lifts her tail up; the male swings his tail smoothly from side to side for cloacal contact, then pumps it up and down beneath the female's while fluttering his wings. Resplendent Quetzals appear to be considerably more discreet, and their copulatory behaviour is little observed: in one case, involving a nest-building pair, the female flew to a tall tree about 100 m distant, whereupon the male followed and, among dense epiphytes in the crook of a branch, briefly mounted her.

The question as to whether trogons line their nests is unresolved. Although most evidence suggests that they do not, there is a record of lining material being carried, and it may be that those species which nest at higher elevations habitually add material to the bottom of cavities. As with many other near-passerines, however, the heels of young trogonids, including the upland quetzals, are covered with numerous prominent sharp papillae to protect them from the abrasive effects of the woody floor, which suggests that nest-lining is unusual.

Trogons lay two to four well-rounded, slightly glossy eggs, which become increasingly dirty as incubation proceeds. They are usually an unspotted white or cream in colour, but sometimes very pale buffish, greyish or greenish. Eggs of quetzals are apparently pale blue, but those of *Temnotrogon* are pale green and the eggs of *Priotelus* are white. A gap of two or, sometimes, three days between eggs has been recorded for the Neotropical species, although a 24-hour laying interval is known for the Narina Trogon in Africa. Eggs may be unattended during the night following completion of the clutch, but thereafter they are kept covered almost continuously. The incubation schedule is fairly simple. The male, even that of the Resplendent Quetzal, no matter how long his tail, undertakes one long session each day, while the female sits for the rest of the time, including at night. Only in the case of Africa's Bare-cheeked Trogon has it been reported that the male plays no part in incubation, but the situation in Asia remains unknown. An incubation period of 16-17 days has been noted for the Narina Trogon, 17 for the Violaceous, and 18 or a little more for the Black-throated, with 18-19 for the Resplendent Quetzal and 19 days for the Mountain and Black-headed Trogons.

For the smaller species, nestling periods of about 16 days are known. Mountain Trogons fledge at 15-16 days and Black-headed at 16-17, but the larger Resplendent Quetzals take at least 23 and often even 30 days. The young of Baird's Trogon remain in the nest for 25 days, far longer than do those of certain other small and middle-sized trogons, this being possibly correlated with the greater security provided by the first species' well-en-

All trogons are cavity-nesters. Natural tree holes and old woodpecker nests may be used, or the birds may dig their own cavities in decaying stumps or in the nests of social insects, commonly termites. More rarely, cacti and tree-fern trunks are excavated, or the hollows in epiphyte roots are enlarged. Finding a suitable tree site is often a major problem for a trogon pair; the selected stump is often too hard to attack, or so soft that it crumbles away. The male appears to choose the site and, by calling, attracts a female to solicit her approval and subsequent collaboration. The Lattice-tailed Trogon is one of the few species with a known courtship ritual: both partners display the colourful rump, uppertail-coverts and vent, and fan out the latticed outer tail feathers while folding them inwards, so that they overlap the central tail.

[Trogon clathratus,  
Costa Rica.

Photo: Michael Gore]





While many trogon species excavate a short upward-sloping tunnel leading to an interior nest-chamber, others, including the quetzals, dig out more open niches, and much of the sitting bird is then plainly visible. Generally, both sexes incubate. It was widely believed that the male Resplendent Quetzal faced the back of the cavity, to allow the long tail-streamers to hang outside. In fact, he turns to face the front, so that, as shown here, the tail feathers are curled around at an improbable angle.

[*Pharomachrus mocinno costaricensis*, Talamanca Range, La Muerte, Costa Rica. Photo: Kevin Schafer]

closed nest; yet this is also the nestling period of the medium-sized Narina Trogon. Nestlings from clutches of four eggs may be quite different in size, apparently because incubation begins with the first egg, or at least it has been found to in the case of the Surucua Trogon. Both parents provide food, but the male generally takes on the greater share of this duty, the female spending more time attending the brood. At the nest of a Violaceous Trogon, the chicks were brooded by both parents for periods of 0.5-1.5 hours up to the age of eight days, after which the female covered them at night for a further two days; from the tenth day they were not brooded at all. A similar pattern exists with the Resplendent Quetzal: one or other parent remains in the nest for 60-95% of daylight hours during the first six to eight days after the hatch; brooding then falls off rapidly, but the adults spend much time near the nest, so that, even late in the cycle, the nest is attended for 20-40% of the day.

All trogon chicks hatch blind and naked. The acquisition of feathers is much more rapid in the upland-nesting Mountain Trogon, the young of which break sheath at around a week, than in the lowland Black-headed Trogon, where the nestlings take twice as long to do so, meanwhile bristling "like little porcupines".

In the relatively well-studied Resplendent Quetzal, the parents at first keep the nest clean, removing and apparently swallowing all droppings. When the chicks are two days old, the sheaths of their body feathers and flight-feathers begin to emerge. At eight days they can open their eyes, although it may sometimes take rather longer for this stage to be reached, and the feathers of the body begin escaping, but those of the head do not do so until day 13. At ten days the remiges and rectrices begin to escape, and at eleven days buffy spots appear on the wing-coverts. At 14 days the chick's body is well covered, and thereafter green becomes more prominent in the plumage. The feathers of the upper dorsal tract are much slower to emerge than those of the lower, appearing only at 16 days, but they are golden-green; by 18 days green-tipped feathers are visible on the scapulars. During the last ten days or so of occupancy the parents do not clean the nest, and a debris of seeds, beetle remains, snail shells and excrement builds up. When one of two nestling quetzals fledged before the other, the female cared for it while the second bird was tended in the nest for two more days by the male; when the second chick fledged, the family united as a party of four.

Nestling Narina Trogons utter a ventriloquial "weee-er" begging call, wheezing excitedly when the adult arrives with food. When disturbed, blind nestlings of this species assume a very

upright posture, with the bill vertical. After their eyes open, however, they hiss like snakes at an intruder, snapping the bill and opening it to waggle the tongue from side to side, a type of anti-predator behaviour observed also from a recently fledged juvenile. Fledglings are fed by both parents until the flight-feathers are fully grown, at about 60 days. The young stay near their parents for several months, and are occasionally fed by them.

Among trogons in general, second broods have not often been recorded. In the case of Resplendent Quetzals, however, they are relatively frequent, although not usually produced in the same nest. In French Guiana, a pair of White-tailed Trogons occupied the same nest-site in January-March and in August in one year. After nest predation, trogons will attempt to re-nest at a fresh site.

Nest losses suffered by trogons are generally high. Ants are a common cause of desertion, while squirrels and snakes take eggs and nestlings. In Resplendent Quetzals, nest failure is frequently high, as much as 67-78% in one study, probably owing chiefly to predation by the short-tailed weasel (*Mustela frenata*); squirrels, toucanets, snakes and botflies (*Gasterophilidae*), as well as some other larger mammals (*Mustelidae*, *Procyonidae*, *Felidae*, *Didelphidae*, *Cebidae*), may also take a toll. The breeding success of Narina Trogons, too, is often poor as a result of predation: at eight nests studied, only four young reached independence, with fledglings being killed by the African Goshawk (*Accipiter tachiro*), African Little Sparrowhawk (*Accipiter minullus*), Ovambo Sparrowhawk (*Accipiter ovampensis*) and, probably, African Wood-owl (*Strix woodfordii*). Trogon nests also fail because of flooding of the cavity, collapse of the snag housing the cavity, and human disturbance.

One of the more remarkable aspects of the breeding cycle is the insanitary condition that develops in the nest. In spite of the porosity of the rotten wood or the termite nesting material, faeces wet the bottom of the cavity and, as they accumulate, they exude a repugnant odour of rotting meat that attracts flies, the larvae of which develop there in profusion. Ostensibly, this ought to be highly disadvantageous to the nestlings, but it is conceivable that the smell acts as a deterrent to would-be predators.

## Movements

For the most part, the Trogonidae show little evidence of migratory behaviour. As denizens of the lower storeys of the forest, some species are relatively easy to net, but their short tarsi make



A montane species of Central and South America, the Collared Trogon is a middle-storey inhabitant of the edges of tropical forest. Although it generally prefers a shallow niche as a nest-site, it will at times select a more enclosed cavity like this one. Little evidence exists that trogons line their nests, but the question is still under debate. Both parents share the tasks of excavation, incubation and brood-feeding. In most trogon species, the male commonly undertakes one long incubating stint, while the female sits for the rest of the time and throughout at night. The Collared Trogon is, in fact, more insectivorous than most other Neotropical trogons, but, even in cases where the adult is more of a fruit-eater, the chicks are fed mostly on insects, at least for the first few days of their lives. Although diligent in their attendance to the young, trogon parents are not renowned for their good housekeeping habits. Droppings are left in the nest, where, along with rotting food remains, they soon form an evil-smelling soggy mess alive with flies and their larvae. Perhaps somewhat surprisingly, these insalubrious conditions do not seem to harm the nestlings. Nevertheless, nest losses are high, largely as a result of predation by other animals; the nest may also become flooded, or the whole nest stump may collapse. Human interference is also a contributory factor to breeding failure in some areas.



[Trogon collaris collaris,  
Manu National Park, Peru.  
Photo: Günter Ziesler]



For birds with a bill ill-suited to chiselling into even unsound wood, a termitarium may offer a better option as a nest-site, though the structure must be occupied by the insects for it to be strong enough to withstand excavation. Unlike some of its more adaptable congeners, the White-tailed Trogon nests almost exclusively in arboreal termitaria. Both partners excavate a rounded chamber in the centre of the termitarium, with a short upward-sloping entrance. They work quickly and probably eat the insects, which unceasingly try to repair the damage. When the trogons' work is done, the termites obligingly seal off the passages leading from the chamber, and appear not to bother their uninvited guests.

[Trogon viridis viridis, Trinidad.  
Photo: M. D. England/Ardea]

them very difficult to ring. Some ringing has, however, been carried out in Peninsular Malaysia, and this has shown that the birds can be very sedentary. A Diard's Trogon was caught at the same site at three-monthly intervals over a period of 18 months, and the same happened with a Cinnamon-rumped Trogon over 22 months.

The assumption is that most trogonids are in this mould. Over smaller time frames, other Asian species, such as the Red-headed, Orange-breasted and Philippine Trogons (*Harpactes ardens*), have also been found to possess very limited territories or daily ranges. Field observations show that a pair can usually be found at a known site after a little patient search or waiting, with a pursued individual normally doubling back to its original perch after only 100-200 m. While this is less a sign of sedentariness than one of territoriality, it does tend to conform with the general impression given by most trogons, on all three continents: namely, that their presence is highly predictable in certain places throughout the year.

Inevitably, even among sedentary species, there must be some dispersal at least by young birds, with individuals occasionally wandering outside their usual areas. This has been noted most clearly for Africa's Bar-tailed Trogons, which turn up in isolated forest patches both inside and outside the breeding season, suggesting strong exploratory behaviour. The same thing may well happen just as much with other trogons, but it is perhaps more detectable in the Bar-tailed owing to the greater fragmentation and restriction of that species' habitat. Nevertheless, the poor performance of trogons in colonizing islands relatively close to major landmasses is evidence of the family's general lack of vagility.

Perhaps the most widespread migratory phenomenon among trogons is the seasonal shift in elevation shown by the montane species or populations of species. This is suspected in several Asian forms, notably Ward's Trogon, and evidence of its occurrence has been accumulated for at least eight Neotropical species, including two quetzals. Indeed, radio-telemetry work on the Resplendent Quetzal in Costa Rica has revealed a complex pattern of movement out of the higher mountain forest in July, after the breeding season. The birds follow fruiting events at lower elevations and spend several months on the Pacific slope, before

crossing to the Atlantic slope for a further couple of months, and then returning uphill to their breeding forest in January. Similar types of displacement are now being documented for that species in Mexico, and it seems highly likely that all four montane species of quetzal will show such behaviour.

Latitudinal displacements are exhibited by a few species, but assumptions made in past years that some trogons migrate may have been based simply on a reduction in the birds' detectability. The Narina Trogon certainly makes local seasonal movements in many parts of its range, and in the Zimbabwean savanna it is believed to be a breeding visitor in the period from November to February, the speculation being that the birds in question retreat to the Mozambique coast for the rest of the year, or at least part of it. The most northerly and southerly populations of trogonids in the New World, the Elegant Trogon and Eared Quetzal in the north and the Surucua Trogon in the south, appear to undertake short-distance migrations into warmer areas in the non-breeding period, although the documentation of this is still very weak.

### Relationship with Man

Trogons and quetzals are widely regarded as among the most beautiful of birds, and they commonly figure in advertisements for birdwatching holidays and, indeed, in any kind of pictorial publicity for the tropical-forest habitats which they occupy. Resplendent Quetzals are of such legendary beauty that they are one of the main target species of ecotourism in Central America, and hotel-proprietors and landowners in some parts of the species' range have good cause to be grateful that their properties happen to lie in or adjacent to the quetzal's cloudforest haunts.

Nevertheless, trogons remain remarkably little known. Owing to their habits and their diet, they are difficult to trap and unsuited to captivity, and as a consequence they are largely ignored by the cagebird trade. A trio of species, the Golden-headed and Resplendent Quetzals and the White-tailed Trogon, have been bred in captivity, but basically the family remains almost unknown in aviculture. Moreover, were it not for the detailed observations on most Central American species by the veteran ornithologist Alexander Skutch, our general understanding of the natural history of



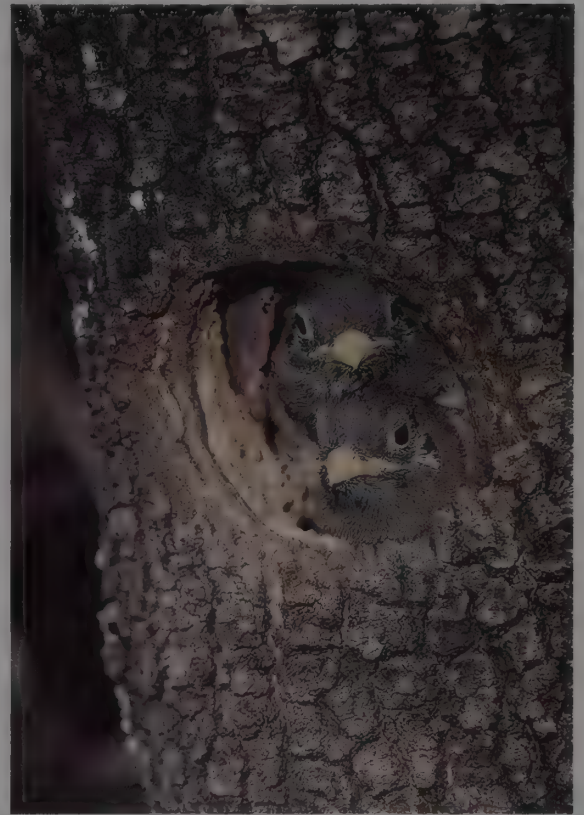
Two alert *Elegant Trogon* chicks peer out of their nest in an old woodpecker hole. At the northernmost limit of this species' range, the great majority of its nests have been found in similar pre-existing hollows; in other areas, it also excavates its own cavities in low rotting trunks. These chicks appear to be well feathered and nearly ready to fly. The plumage resembles that of the adult female, the lower one even showing an incipient white bar on the ear-coverts. The young of all trogons hatch blind and naked; they are brooded assiduously by their parents. *Elegant Trogons* leave the nest after 15-16 days, which appears to be the normal nestling period for the smaller members of this family.

[*Trogon elegans goldmani*,  
Madera Canyon,  
Arizona, USA.  
Photo: S. & S. Rucker/  
VIREO]

the Trogonidae would be fragmentary and negligible. However familiar their calls may be, the birds themselves are often so retiring that they remain little known even to local communities. A nice example of this comes from Tobago: in 1963, when some Collared Trogons were blown out of the forest by a fearsome hurricane, they were not recognized as native creatures but were thought to be birds-of-paradise (*Paradisaeidae*) that had been released on the island several decades earlier.

There is, however, at least one human society whose esteem of trogons is a cornerstone of its culture. In south-west Borneo, the Iban, or sea-dayaks, possess an elaborate system of augury (divination by omens) which governs their lives closely and which involves deep reverence for the voices of a few sacred, benign bird species, among them the Scarlet-rumped and Diard's Trogons. Whenever these birds are heard or seen, it is believed that the gods have something advantageous to communicate. The Scarlet-rumped Trogon sounds like a man laughing, so that, if one is heard on a trading or hunting expedition, it predicts a happy outcome to the enterprise; moreover, the species' bright red breast is a symbol of success and renown. Diard's Trogon sounds like a man in neutral conversation or, when calling in alarm, like a person speaking sharply to another, or like the sound of blood rattling from the cut throat of a quarry; so, the species is called a *burung darah* ("bird of blood") and a *burung rabun* ("cryptic bird"). Its song signals the inability of a quarry to see its pursuer, or the inability of an enemy to hit its targets, and in the evening it has the effect of shutting the eyes of evil spirits.

The most celebrated trogon in human culture is, however, the Resplendent Quetzal, which for centuries dominated the traditions and beliefs of the Maya and Aztec peoples of Central America. Quetzalcoatl, the cultural force for good for both Mayas and Aztecs, was symbolized by the head of a serpent adorned with the feathers of a Resplendent Quetzal. The rulers in both cultures required tributes and head-dresses made of quetzal tail-streamers, but, since the birds were considered sacred, the penalty for killing one was death. The quetzals were therefore freed after the long plumes had been removed, so that, despite the considerable numbers captured, the population suffered no adverse effects (see Status and Conservation). According to Aztec legend, Quetzalcoatl was supposed to return in 1519 as god-king to rule them. Consequently, it is not surpris-



ing that, when the Spanish conquistador Cortez in that year sailed into Vera Cruz harbour, the first gift that Montezuma sent him was a magnificent head-dress of quetzal plumes.

Quetzalcoatl's association with the Mayan god Kukulcan has recently been highlighted by the claim that the pyramid at Chichen Itza, in Mexico, was constructed in such a manner that sharp sounds made inside it produce an echo that mimics the call of the Resplendent Quetzal. The echo is produced by the

An adult *Collared Trogon* flies off, having just fed a large arthropod to a perched fledgling. The behaviour of trogons in this final stage of the breeding cycle is not well known. The young appear to be fed by the parents until their flight-feathers are fully grown, and sporadically thereafter, but they may not disperse until several months later. Juveniles of most Neotropical species are dull brown, with traces of adult colouring, and much spotting on the wings.

Once the first basic plumage is acquired, the sex of the immature is recognizable, but the undertail pattern may differ from the adult's. Full adult plumage is gained in about one year.

[*Trogon collaris exoptatus*,  
Henri Pittier National Park,  
Venezuela.  
Photo: Bernard van  
Elegem]







faces of steps in limestone staircases, and it is suggested that it represents the spirit of the Mayas. This idea has been greeted with scepticism in some learned quarters, but echoes were often associated with spirits, and the central importance of the quetzal in Mayan beliefs makes it entirely plausible that the pyramid-builders deliberately included such a device as a further means of totemizing the species.

The legendary status of the Resplendent Quetzal survives in various forms today. The name "quetzal" comes from the Aztec *quetzalli*, originally meaning tail feather, and by transference "precious" or "beautiful". Thus it is that the unit of monetary currency in present-day Guatemala is the quetzal. Until fairly recently, old men of that country would kill a quetzal and parade it through the streets, so as to assure themselves another year of health. One small community annually wraps its statue of St Joseph in quetzal plumes and carries it through the village in solemn procession.

### Status and Conservation

In general, trogons are relatively common birds, living at fairly high densities compared with some other species of tropical forest. This means that, even where they have restricted ranges, the species in question are often sufficiently numerous to be in relatively little danger. There are, in any case, rather few restricted-range species.

On the assumption that the form "*aurantiventris*" is a morph of the Collared Trogon, rather than a full species, and accepting the separate species status of the Javan and Sumatran Trogons, the number of trogonids which meet the BirdLife International criteria of restricted-range species is eight. These are Whitehead's Trogon in montane north Borneo, the Javan and the Sumatran Trogons, confined to those respective islands, Ward's Trogon in the Himalayas and east to Vietnam, the Hispaniolan Trogon, found nowhere but on the Caribbean island of Hispaniola, Baird's and the Lattice-tailed Trogons in Central America, and the White-eyed Trogon in north-west Colombia. In 1994, only Ward's Trogon among these eight was judged to be at risk, owing to substantial forest loss within its range, but there are now known

to be areas where it appears to be, for the time being, relatively secure. Similarly, the only other trogon considered threatened in 1994, the Eared Quetzal, is now known to be commoner and more widespread than was then understood. Both species have now been reclassified as Near-threatened.

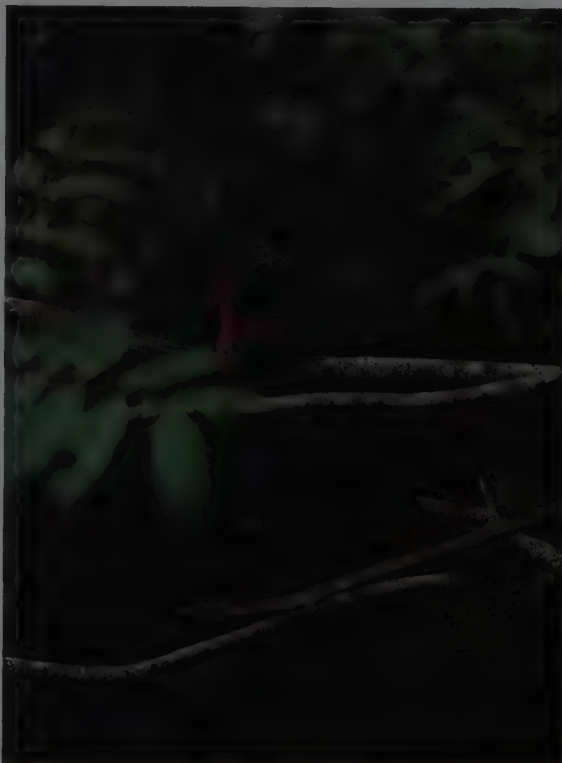
Nevertheless, it is inevitable that the trogons, since they inhabit tropical forest, are declining in numbers on all continents. They are birds of the understorey which, as repeated study has shown, are sensitive to partial cutting, or logging. All the Asian species suffered losses of numbers after logging in Peninsular Malaysia, and indeed trogons are one of the key avian groups, along with flycatchers, woodpeckers and wren-babblers (Timaliidae), which in Sabah, Borneo, become comparatively rare following commercial timber extraction. This finding is not entirely matched by experience in South America, where several studies have shown that, while the Pavonine Quetzal, the Black-tailed Trogon and, especially, the Black-throated Trogon are highly sensitive to selective logging, the status of the White-tailed and, in particular, the Violaceous Trogons may be improved following such activities. In general, however, the effect is certainly one of net loss. Moreover, even in situations where habitat quality is not compromised, the confiding nature, or, as the old writers put it, the stupidity, of trogonids has been blamed for the great diminution in their numbers near human settlements. In Brazil, for example, Sick asserted that trogons have entirely disappeared from the forest areas around Rio de Janeiro as a result of hunting.

In 1999, Skutch reported that his "modest tract of tropical rain forest" in Costa Rica had been steadily encroached upon and reduced in size, but that it still held the four species of trogon that he first encountered in it 40 years earlier. Of all the woodland birds there, however, trogons have the greatest difficulty when it comes to finding sites for their nests. Certainly, any kind of forest management which eliminates rotting stumps will make it much more difficult for tree-nesting species of trogon to find appropriate nesting sites. On the other hand, as noted earlier (see Breeding), the density of suitable nest-sites for Resplendent Quetzals appears to exceed the density of the birds themselves; and termitarium-nesting species in Peru also seem to be under no pressure from this problem. Black-tailed Trogons having around 60 suitably sized termitaria per 5-ha territory to choose from.

As the preceding three paragraphs suggest, there is a seesaw of judgement about the current status and circumstances of the

*Loss of forest habitat through logging is undoubtedly the major cause of the current decline in trogon numbers almost everywhere. Hunting and other forms of human interference may also be partially responsible. At present, however, no trogonid is classed as threatened. Even those with restricted ranges appear, for the most part, to be maintaining acceptably stable population levels. The poorly known Whitehead's Trogon, found only in mountain areas at up to 1500 m in north Borneo, is scarce throughout its range, and possibly declining locally; it is classified as Near-threatened. Its precise status is difficult to gauge, but at least its habitat seems relatively secure for the present.*

[*Harpactes whiteheadi*, Mount Kinabalu, Sabah. Photo: Bernard van Elegen]



*A high-altitude species rarely seen below 1500 m, Ward's Trogon is sparsely distributed throughout its restricted range in the eastern Himalayas, north Myanmar and adjacent south China and Tonkin, where it inhabits the lower storey of tall forest. It was listed as Vulnerable as recently as 1994, having suffered severe habitat destruction. Since then, however, hitherto unknown populations have been discovered, and its status has been modified to that of Near-threatened. Even though its immediate future now gives less cause for concern, continued and widespread clearance and degradation of forest nevertheless remain significant problems.*

[*Harpactes wardi*, near Limithang, east Bhutan. Photo: John & Jemi Holmes]



trogons as a group. With any poorly studied family of tropical-forest birds, it is difficult to gauge the recent, current and future impacts of various developments on the conservation status of its constituent taxa, especially in the case of the more widespread species, for which insights at the local level may not be a strong guide to the broader situation. The plight of Indonesian lowland forest is beginning to emerge as particularly dire, and it may well be that some species which have long been thought secure will prove to be in need of much attention. The Cinnamon-rumped Trogon, a species that is already mysteriously rare in Sumatra, could fall into this last category, and it is one of ten trogonids that now appears on the Near-threatened list.

At present, it is the Resplendent Quetzal that may be, after all, the most threatened trogonid of the modern era. This is ironic, considering the levels of pressure which the species has managed to endure over the centuries. At the height of the Aztec empire, five provinces which contained cloudforest were compelled to furnish tributes in the form of as many as 2480 "bunches" or "handfuls" of mostly tail-streamers from Resplendent Quetzals. If it is assumed that each handful contained ten to fifty such feathers, with four from each bird, this would have meant a harvest of 6200-31,000 Resplendent Quetzals per year! Even if the lives of the birds were spared, the figure is still astonishing, and indicates that the species must have been very much more abundant in pre-Columbian times than it is today. Furthermore, and despite the edict of death on those who killed them, it seems inevitable that a large proportion of quetzals might have been seriously injured in the capture/plucking process.

In more recent times, the trade in avian feathers again took its toll. For several decades during the great Victorian fashion for plumes, as many as 800 quetzals were exported annually from Guatemala, and the trade must have been just as intense in other parts of the species' range. Even as recently as 1956-1966, as many as 100 pairs per year were being exported from Costa Rica for zoos and private aviaries, the price at that time being \$200 a pair. In 1973, a single Costa Rican dealer claimed to have exported 100 birds, and it was in response to such pressure that the Resplendent Quetzal was placed on Appendix I of CITES.

Trogons appear to be particularly sensitive to human disturbance, especially during the breeding season, and this has become an increasing problem in recent years. The activities of birdwatchers and tourists, understandably desirous of seeing these beautiful birds,

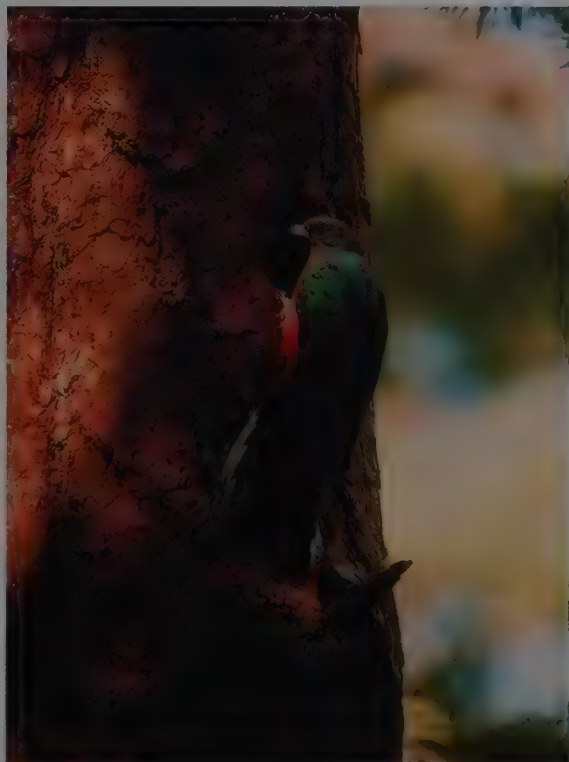


has given cause for serious concern in some areas. For example, the use of tape recordings to lure the birds into view, or to locate their nesting sites, has been held responsible for the almost total reproductive failure of the Elegant Trogon in Arizona, the most northerly point reached by the Trogonidae in the New World.

It is, however, inevitably habitat destruction that is the main concern nowadays among conservationists. Clearance of cloudforest for farming purposes, including shifting agriculture, cattle-ranching and the growing of cash-crops, is a major problem in some areas, reaching to altitudes as high as 1500-2000 m, and it is compounded by accidental fires and deliberate exploitation for timber, roofing, firewood and charcoal. Despite a series of reserves now established throughout the breeding range of the species, the real problem lies in habitat destruction farther downslope. With the discovery that the quetzals wander to lower-lying areas in pursuit of fruiting lauraceous trees, it has suddenly become apparent that forest fragments outside protected areas are vitally important for the survival of the Resplendent Quetzal. The larger fragments are the more important, since they hold more of the sought-after trees in fruit. Maintaining lauraceous diversity in these fragments will be essential for the long-term local and, ultimately, global survival of the quetzal. The tourist industry related to the Resplendent Quetzal around Monteverde alone includes over 80 businesses and generates over US\$5,000,000 annually in local revenue, so the incentives to establish corridors and private woodlot patches for the species are very high indeed.

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Another species that is classed as Near-threatened is the Hispaniolan Trogon, which is, as its name suggests, confined to the Caribbean island of Hispaniola.

Formerly common in the mountain rainforest on the island, it is now only locally numerous in unaltered habitat in the Dominican Republic. In Haiti, where this attractive trogon can still be found in certain massifs, it is considered to be threatened, as its numbers are dwindling.

The main problem throughout Hispaniola is the destruction and deterioration of forest habitat; in the Dominican Republic, damage is sometimes caused by fires started by illegal Haitian immigrants. Known commonly as "papagayo", it is also hunted for food.

[*Temnotrogon roseigaster*, Sierra de Bahoruco National Park, Dominican Republic. Photo: Eladio Fernández]

The Eared Quetzal is more or less confined to the highlands of Mexico, where it was previously known from very few breeding sites; it was considered rare, and much affected by logging and a consequent lack of suitable nesting trees.

In 1995, however, extensive searching in Sierra Madre for the presumed extinct Imperial Woodpecker (*Campephilus imperialis*) revealed that the Eared Quetzal was common in suitable habitat and little affected by logging, being found at no fewer than 55 sites. In the light of this heartening new evidence, the species is now listed as Near-threatened, rather than Endangered.

[*Euptilotis neoxenus*, Mesa las Guacamayas, Chihuahua, Mexico. Photo: Martjan Lammertink]





## Subfamily APALODERMATINAE

### Genus *APALODERMA* Swainson, 1833

#### 1. Narina Trogon

##### *Apaloderma narina*

**French:** Trogon narina

**German:** Narinatrogon

**Spanish:** Trogón de Narina

**Taxonomy.** *Trogon Narina* Stephens, 1815. Knysna District, Cape Province.

Six subspecies recognized.

**Subspecies and Distribution.**

*A. n. constantia* Sharpe & Ussher, 1872 - Guinea and Sierra Leone E to Nigeria.

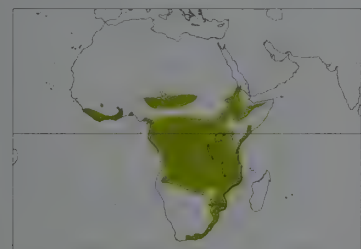
*A. n. arcanum* Clancey, 1959 - L Chad E to Ethiopia and Somalia, and S to N fringes of equatorial forest E to N Kenya.

*A. n. brachyurum* Chapin, 1923 - S Cameroon E through N Congo Basin to Rift Valley.

*A. n. rufiventre* Dubois, 1896 - S of R Congo mouth E to S Uganda, W Tanzania and N Malawi, and S to N Namibia, N Botswana, Zambia, and E highlands of Zimbabwe and adjacent Mozambique.

*A. n. littorale* van Someren, 1931 - SW Somalia, E Kenya, E Tanzania, N Mozambique, S Malawi and Zimbabwe (Mt Selinda).

*A. n. narina* (Stephens, 1815) - S Cape E to S Mozambique; winters N to E Zimbabwe, Malawi and N & C Mozambique (N of R Save).



**Descriptive notes.** 30-32 cm; 51-95 g. Male of nominate race has bill yellow with pale blue flashes at base and under eye; otherwise head to middle breast and upperparts brilliant metallic green, mid-breast to vent geranium-red; wingpanel finely barred blackish and pale grey or whitish; uppertail dark blue-green, with 3 outer feathers white, undertail largely white; underwing with conspicuous white bar. Female brown on face and throat, pinkish-grey on breast, red on belly and vent; bare facial skin blue or bronzy blue-green. Juvenile like female, but with less pink on belly, white-tipped inner secondaries. Race *littorale* smaller than nominate, with greenish orbital ring, bronzy wash above and paler red below; *brachyurum* also smaller, shorter-tailed, male slightly bluer green, especially on crown and breast, with dull yellowish-green bare face patches, female with grey wash on face and breast; *rufiventre* bronzy green above, deeper red below than nominate; *arcanum* like *rufiventre* but longer-tailed; *constantia* has yellow bare face patches, greener bill, more white than blackish in wingpanel, which extends further up coverts, purplish uppertail, more white on outer tail than in *brachyurum*. VOICE. Territorial call of male a series of growling double hoots: "whoou-whoou" or "roo-kóok", hardly audible at first, then rising to climax. In courtship a rapidly repeated low "kuk"; various rolling growls in aggression.

**Habitat.** Generally in mid-stratum of rainforest, gallery forest and savanna woodland. In W Africa in primary forest, also logged and secondary forest and, more rarely, forestry plantation and wooded savanna, and often along rivers and creeks; in Gabon, separates ecologically from *A. aequatoriale* by occupying more open, broken-canopy woodland, often where primary habitats disturbed by man (e.g. old villages and overgrown plantations), but also storm-struck areas, with highest density in montane forest. In Rwanda (Nyungwe Forest) avoids closed forest, preferring thickets under broken canopy, edges, mixed bamboo-*Macaranga* forest, pine plantations. In E Africa mainly in low and mid-level forest and rich woodland, also in some highland forests and, in N Somalia, juniper hill woodland, to 2200 m; in Ethiopia in *Podocarpus* and *Hypericum* forest at up to 3500 m, but also arid woodland and thornbush. In SC & S Africa in evergreen and riparian forest, dense scrub and thickets in valleys, forest-woodland mosaic, occasionally *Brachystegia* and mopane (*Colophospermum mopane*) woodland, semi-evergreen and deciduous thicket and transition woodland (moist miombo with some evergreen understorey), moist thornveld, coastal bush, valley bushveld (especially *Euphorbia*), wattle plantations and well-wooded suburban gardens, at 50-1600 m.

**Food and Feeding.** Mainly insects, particularly smooth-skinned caterpillars (Lepidoptera: Papilionidae, Sphingidae, Charaxidae), rarely hairy ones; large green Orthoptera, mantises, cicadas, beetles, bugs, stick-insects, flying termites, adult butterflies and moths; also spiders, and occasionally small terrestrial and arboreal lizards (including chameleons) and frogs. At one nest, stick-insects were main item fed to nestlings; in *Euphorbia* woodland in E Cape, cicadas assumed to be a main prey. Occasionally joins mixed-species flocks.

**Breeding.** Feeding young in Apr in Ivory Coast; possibly throughout year in Gabon (young seen in Aug, Nov and Mar) and Zaire (breeding females taken Jan, Apr and Sept); Mar-Jun in Ethiopia and Nov in Uganda; in Kenya, all months except Jan, Jul and Sept, peak Apr-Jun (in and just after long rains), some breeding also if short rains good; Dec in Angola, Dec-Jan in Zimbabwe, and Oct-Jan in Mozambique and South Africa. Monogamous, with strong pair-bond; territorial throughout year, territory 1-2 ha, defended by male. Nest in rotted hole or other natural cavity in living or dead tree or stump, 1-12 m up in vertical limb; cavity may be used in successive years. Eggs 1-4 in South Africa, 2-3 in Kenya; incubation 16-17 days in South Africa, by female, but 18 and 21 days reported in Kenya; nestling period c. 25 days.

**Movements.** Generally sedentary in W Africa, pair remaining virtually all the time within small territory; detectability lower in May-Jul in Tai National Park, Ivory Coast, but not necessarily owing to emigration. In E & S, some diurnal and nocturnal migration occurs; race *littorale* could be non-breeding migrant to coastal forest in Kenya, and nominate shows altitudinal migration to lower levels in wet seasons; at least local wandering in Malawi and Zambia, with birds sometimes found considerable distances from suitable habitat at start of rainy season; overlap of subspecies in parts of E & S Africa explained as partial dry-season emigration; in Zimbabwean savanna W from Kariba Basin may occur only Nov-Feb as breeding summer migrant, possibly coming from Mozambique littoral; in E Cape moves down rivers in search of adequate cover, and in Transvaal there is downward movement in winter.

**Status and Conservation.** Not globally threatened. Generally uncommon but very widespread, in most forested parts of sub-Saharan Africa. In W, widespread but locally very patchy, e.g. in Ivory Coast very rare in Yapo Forest, yet one of most commonly recorded species in Tai National Park; uncommon in Nigeria; common in Gabon, where on one mountain density may be 1 pair/10 ha. Present in Bamingui-Bangoran National Park and the Dzanga Reserves, Central African Republic; in Kouilou Basin, Congo, common only on higher hills of the C Mayombe; common in lowland and temperate forest in E Zaire, present in e.g. Upemba National Park. Found in 8 national parks in Uganda. In Ethiopia, uncommon to common in various habitats; in Somalia, rare in NW but locally fairly common in SE. Widespread but uncommon in E Africa, but densities of 5 pairs/8 ha of forest (Nairobi, Kenya), and fairly common in Arusha and Lake Manyara National Parks in Tanzania; scarce in Serengeti National Park. Common in Malawi, and locally abundant in Zambia. Tiny population in riverine forest in N Botswana and Caprivi Strip at risk from impact of elephants and humans on riparian habitat. Locally common in Transvaal.

**Bibliography.** Allport *et al.* (1989), Anon. (1982), Archer & Godman (1937-1961), Ash & Miskell (1998), Bannerman (1933, 1953), Barbour & Steyn (1972), Bennun (1986), Benson (1953, 1982), Benson & Benson (1977), Benson & Irwin (1967), Benson & White (1957), Benson *et al.* (1971), Britton (1980), Brooke (1994b), Brosset (1983), Brosset & Énard (1986), Brown (1970, 1975), Brown & Britton (1980), Cave & Macdonald (1955), Chapin (1939), Cheke & Walsh (1996), Chenaux-Repond (1985), Christy & Clarke (1994), Clancey (1959a, 1971a, 1996), Colston & Curry-Lindahl (1986), Cunningham-van Someren (1973, 1975), Dean (2000), Demey & Fishpool (1994), Dowsett (1990), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Dowsett-Lemaire (1989), Elgood *et al.* (1994), Field (1999), Friedmann (1930a), Fry *et al.* (1988), Gartshore *et al.* (1995), Gatter (1997), Ginn *et al.* (1989), Graham & Graham (1982), Grimes (1987), Harcus (1976), Harrison *et al.* (1997), Heinrich (1958), Irwin (1981), Lewis & Pomeroy (1989), Lippens & Wille (1976), Louette (1981b), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Martin *et al.* (1990), Pakenham (1979), Penry (1994), Pinto (1983), Prigogine (1971), Schouteden (1954), Serle (1954), Serle *et al.* (1977), Short *et al.* (1990), Skead (1967), Snow (1978), Steyn (1996a, 1996b), Stuart & Jensen (1985), Tarboton *et al.* (1987), Traylor (1960a, 1963), Urban & Brown (1971), Vincent (1935), Zimmerman *et al.* (1996).

#### 2. Bare-cheeked Trogon

##### *Apaloderma aequatoriale*

**French:** Trogon à joues jaunes

**German:** Gelbwangentrogon

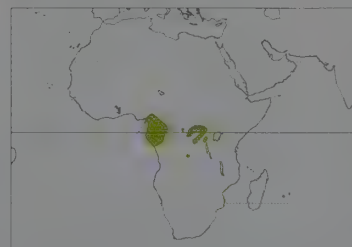
**Spanish:** Trogón Carigualdo

**Other common names:** Yellow-cheeked Trogon

**Taxonomy.** *Hapaloderma aequatoriale* Sharpe, 1901. Efulen, Cameroon.

Monotypic.

**Distribution.** E Nigeria, Cameroon, Equatorial Guinea, Gabon, Congo and Zaire (E to S Uelle District and S to Kasai).



**Descriptive notes.** 28-31 cm. Male has whitish to green bill with yellow base; head to mid-breast and entire upperparts green with blue and golden gloss; yellowish bare facial patch; underparts below mid-breast pinkish-red; wingpanel finely barred pale grey and blackish; uppertail bluish-green, central feathers violet, outer 3 feathers largely white, undertail mostly white. Differs from *A. narina* in slightly smaller size, proportionately shorter tail, face without blue flashes but with bare yellow patch. Female with brown face and throat, breast washed cinnamon-brown. Juvenile like female, but inner secondaries

with large white tips. VOICE. A melancholy descending series of 6-8 pained "chuu" notes; raucous whining notes.

**Habitat.** Primary lowland rainforest, closed-canopy swamp-forest, low-lying liana-rich floodforest, and logged forest where canopy relatively intact. In Gabon always in closed-canopy habitats, which separates it from *A. narina* of more open woodland. Typically, keeps to horizontal lianas and leafless branches 3-8 m up in understorey.

**Food and Feeding.** Insects, mostly large green caterpillars (some hairy), beetles, moths, mantises, and Orthoptera (bush-crickets); also soft-shelled snails (*Helix* spp.). Pursues prey in manner of drongo (*Dicrurus*), even chasing it to the ground.

**Breeding.** Jan in Cameroon; in Gabon in Jan-Feb and Nov, and nest disputes in Aug (thus in wet and dry seasons), suggesting no fixed season; in Zaire in Apr and Aug, with immature in Oct, so protracted; in N chiefly after Jul. Monogamous; territorial, male selects nest and fights for possession. Nest cavity 2-8 m up in rotting tree, unlined. Eggs 2; incubation c. 16 days; nestling period c. 16 days.

**Movements.** Resident; possibly some vagrancy in Dec in Congo.

**Status and Conservation.** Not globally threatened. Fairly common in Korup National Park, Cameroon. Locally common in parts of Gabon, reaching a density of 1 singing male/10 ha. In Congo, present in Odzala and Nouabalé-Ndoki National Parks, reaching density in optimal habitat of 3 pairs/10 ha in former, and common in latter; in Kouilou Basin, common only on higher hills of the C Mayombe.

**Bibliography.** Ash *et al.* (1989), Bannerman (1933, 1953), Brosset (1983), Brosset & Énard (1986), Carroll (1988), Chapin (1939), Christy & Clarke (1994), Dowsett (1989a, 1989b), Dowsett & Dowsett-Lemaire (1991, 1993, 1997), Dowsett & Forbes-Watson (1993), Dowsett-Lemaire & Dowsett (1999), Elgood *et al.* (1994), Fry *et al.* (1988), Lippens & Wille (1976), Louette (1984, 1987), Mackworth-Præd & Grant (1970), Pedersen (1997a, 1997b), Rodewald *et al.* (1994), Sargeant (1993), Schouteden (1954), Snow (1978).

#### 3. Bar-tailed Trogon

##### *Apaloderma vittatum*

**French:** Trogon à queue barrée

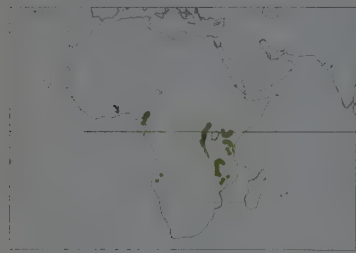
**German:** Bergtrogon

**Spanish:** Trogón Montano

**Taxonomy.** *Hapaloderma vittatum* Shelley, 1882. Mamboio, Tanzania.

Has on occasion been separated in monospecific genus *Heterotrogon*. Population in W half of Africa sometimes separated subspecifically as *camerunense*, and birds from Bioko (Fernando Póo) occasionally further separated as *francisci*, but characters apparently not constant for either of these forms. Monotypic.

**Distribution.** Mountains in SE Nigeria, NW Cameroon, W Angola (Mt Moco); Bioko (Fernando Póo); also Albertine Rift in E Zaire, W Uganda, Rwanda and Burundi, and mountains in Kenya, Tanzania, NE Zambia, Malawi and N Mozambique (Mt Namuli).



**Descriptive notes.** c. 28-30 cm; 55 g. Male with bill yellow or greenish-yellow; patches of bare skin below eye yellow or orange, above eye yellow or grey; head and throat blue-black with bronzy green gloss; breastline violet-blue; upperparts bright green; mid-breast to vent red; wingpanel barred black and grey; uppertail mainly bluish or purplish-black, outer 3 feathers barred black and white, undertail densely barred black and white; underwing with conspicuous white bar. Female has brown head and cinnamon-brown breast. Juvenile white-bellied, with wing-coverts tipped buffy-white.

**VOICE.** Territorial call a series of 7-14 sharp,

high-pitched "wup" or "uyú" notes, increasing in volume, very like that of Freckled Nightjar (*Caprimulgus tristigma*); female utters whining "chee-uu".

**Habitat.** Usually in mid-stratum (4-20 m, but seldom lower than 8 m) of moist montane forest at 900-3000 m, mainly above 1600 m. In Cameroon, has been found in old second growth as well as primary forest, but seemed particularly to favour mountain tops and tree-clad ridges bounding ravines. In Malawi, sometimes in montane grassland and planted pine, presumably as a temporary local displacement. Recorded as low as 600 m in Rubeho Mountains in Tanzania. In Bioko from at least 900 m to 2000 m, including in moss forest and lichen forest.

**Food and Feeding.** Canopy insects, mainly smooth caterpillars, also Orthoptera, moths and beetles. Caterpillars and moths noted as preferred prey in Malawi; caterpillars and grasshoppers recorded in diet in Bioko. Once observed in mixed-species foraging party.

**Breeding.** Nov-Jan in Bioko, Oct and Dec-Feb in Cameroon, Feb-May in Zaire, Mar in Uganda, Nov-Feb in Kenya (in and after short rains), Sept and Nov-Feb in Tanzania; nestling found in Sept in Angola; Oct-Nov in Malawi, with territorial activity Aug-Dec. Probably monogamous; territories in Malawi variable in size, 1-7.5 ha, most birds occasionally visiting small adjacent forest patches to feed, even if territory relatively large (10 ha). Nest is a cavity in a dying tree, usually c. 2 m up (1-1.5 m in Bioko). Eggs 2, sometimes 3; incubation and fledging periods undocumented.

**Movements.** Resident, with some vertical displacement in non-breeding season in all parts of range; also other, very poorly documented local movements. Occasional records of birds in well-watched isolated forest areas suggest extensive non-breeding wandering; some inter-montane movements of up to 100 km from nearest established population. In Malawi, wanderers found at middle or high elevations (1300-2200 m) in Aug-Dec, when territorial defence is most intense, suggest strong exploratory behaviour, birds searching for suitable habitat to settle.

**Status and Conservation.** Not globally threatened. Not uncommon on Obudu Plateau, Nigeria; in Cameroon, locally common on Mt Kupé, less so on five other mountains in W highlands; fairly frequently recorded in Bioko, although shy and difficult to observe, all records coming from primary forest; common at Iombwe, Zaire. Generally uncommon in E Africa: has disappeared in recent years from forest around Nairobi; found in Arusha National Park in Tanzania, and in three national parks in Uganda; in Rwanda, densities in Nyungwe Forest moderate even in most favourable habitat. In Zambia, density as high as 12 pairs/25 ha under closed canopy in Chowo Forest, Nyika Plateau: where canopy discontinuous, often 2-3 pairs/10 ha. Possibly extinct at Chiradzulu, Malawi. Was fairly common on Mt Namuli, Mozambique, in early 1930's, but no recent data.

**Bibliography.** Ash *et al.* (1989), Aspinwall & Beel (1998), Bannerman (1933, 1953), Bennun & Njoroge (1999), Benson (1953, 1982), Benson & Benson (1975, 1977), Benson & Irwin (1967), Britton (1980), Brown & Britton (1980), Chapin (1939), Dean (2000), Dowsett (1980, 1989a, 1990), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dowsett-Lemaire (1989), Dowsett-Lemaire & Dowsett (1984), Elgood *et al.* (1994), Fjeldså *et al.* (1997), Fry *et al.* (1988), Heinrich (1958), Kalina & Baranga (1991), Lewis & Pomeroy (1989), Lippens & Wille (1976), Mackworth-Praed & Grant (1957, 1962, 1970), Moreau & Moreau (1939), Pérez del Val (1996), Pérez del Val *et al.* (1994), Pinto (1983), Prigogine (1971), Schouteden (1954), Serle (1950b, 1954, 1965), Short *et al.* (1990), Snow (1978), Stuart & Jensen (1985, 1986), Traylor (1960a, 1963), Vincent (1935), Zimmerman *et al.* (1996).

## Subfamily HARPACTINAE

### Genus *APALHARPACTES* Bonaparte, 1854

#### 4. Javan Trogon

##### *Apalharpactes reinwardtii*

**French:** Trogon de Reinwardt **German:** Reinwardttrogon **Spanish:** Trogón de Java  
**Other common names:** (Reinwardt's) Blue-tailed Trogon (with *A. mackloti*)

**Taxonomy.** *Trogon reinwardtii* Temminck, 1822, Java.

Genus name sometimes erroneously "emended" to *Hapalarpactes*. This species and *A. mackloti* have usually been placed in genus *Harpactes*, and also treated as conspecific; both differ, however, from *Harpactes* species in plumage coloration and in having a red bill, as well as being the only Asian trogons with metallic tones in plumage; in addition, at least one (*A. mackloti*) has a song quite unlike that of any other trogonids: recent research, as yet unpublished, indicates that present species and *A. mackloti* differ significantly in biometrics, and possibly also in vocalizations, and are probably better treated as separate species forming a superspecies. Monotypic.

**Distribution.** Mountains of W Java.

**Descriptive notes.** 34 cm. Male has yellowish-green head and bluer green upperparts with yellow-barred wingpanel, deep metallic blue tail; yellow throat and belly with pale grey-green breastband; red bill, blue orbital ring, orange feet. Differs from very similar *A. mackloti* in larger size, longer tail, heavier bill, and green rump. Female has wingpanel barred buffier and narrower. **VOICE.** Penetrating hoarse "chierr, chierr" or loud "turrr". Not yet known whether or not present species also performs the song recorded for *A. mackloti*.



**Habitat.** Occurs in lower storey of montane rainforest at altitudes of 900-2500 m, chiefly on lower slopes.

**Food and Feeding.** Diet consists of beetles (including genus *Aegosoma*) and cicadas (including genus *Platylomia*), mostly taken in flight; also takes caterpillars, stick-insects, grasshoppers and bugs; in addition, commonly feeds on fruit, such as figs. Occasionally joins mixed-species flocks.

**Breeding.** Recorded Apr-Jun, Aug, Oct and Dec; a party of 5 birds seen in Nov may have been a family group. Eggs 1-2, possibly 3. No further information available.

**Movements.** Apparently sedentary within its limited range.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in Java and Bali Forests EBA. Since species has hitherto normally been treated as conspecific with *A. mackloti* of Sumatra, its conservation status may need to be reassessed; present only at limited number of sites in Java. Appears uncommon within restricted range; known to be uncommon in Gunung Gede/Pangrango National Park.

**Bibliography.** Andrew (1985, 1992), Hellebrekers & Hoogerwerf (1967), Hoogerwerf (1950a), Inskipp *et al.* (1996), Kraus (1987), MacKinnon (1988), MacKinnon & Philipps (1993), Sargeant (1997), Stattersfield *et al.* (1998), Sujatnika *et al.* (1995), Wheatley (1996).

#### 5. Sumatran Trogon

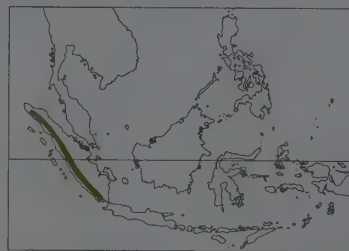
##### *Apalharpactes mackloti*

**French:** Trogon de Sumatra **German:** Macklottrogon **Spanish:** Trogón de Sumatra  
**Other common names:** (Reinwardt's) Blue-tailed/Blue-billed Trogon (with *A. reinwardtii*)

**Taxonomy.** *Trogon Mackloti* S. Müller, 1835, Mount Singgalang, Sumatra.

Genus name sometimes erroneously "emended" to *Hapalarpactes*. Has usually been placed together with *A. reinwardtii* in genus *Harpactes*, and the two treated as conspecific; both differ, however, from *Harpactes* in plumage coloration and in bill colour, and are also the only Asian trogons with metallic tones in plumage; in addition, at least present species has a song quite unlike that of any other trogonids; recent research, as yet unpublished, indicates significant differences between present species and *A. reinwardtii* in biometrics, and possibly also in vocalizations, suggesting that the two are better treated as separate species that form a superspecies. Monotypic.

**Distribution.** Mountains of Sumatra.



**Descriptive notes.** 30 cm. Male has yellowish-green head and bluer green upperparts, yellow-barred wingpanel, deep chestnut rump, deep metallic blue tail; yellow throat and belly, pale greyish-green breastband; red bill, blue orbital ring, orange feet. Very similar to *A. reinwardtii*, from which differs in smaller size, shorter tail, smaller bill, and chestnut rump. Female has barring on wingpanel buffier and narrower. **VOICE.** Penetrating hoarse "chierr, chierr" or loud "turrr", not apparently differing from that of *A. reinwardtii*; song distinctive, a high whistled "wiwi wheeerr-lu", repeated every few seconds.

**Habitat.** Occupies lower storey of montane rainforest, chiefly on lower slopes, in altitude range of 750-2200 m.

**Food and Feeding.** Green caterpillars, grasshoppers, stick-insects, beetles, bugs; also fruits; once a lizard 10 cm long, taken from the ground.

**Breeding.** Mar; immatures collected in May and Jun. Eggs 1-2. No other information.

**Movements.** Apparently sedentary.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in Sumatra and Peninsular Malaysia EBA. Uncommon within range; formerly judged the least rare of all trogons on Sumatra, and very common on Kerinci.

**Bibliography.** de Beaufort & de Bussy (1919), Chasen & Hoogerwerf (1941), Holden (1997), MacKinnon & Philipps (1993), van Marle & Voous (1988), Meyer de Schauensee & Ripley (1940), Robinson & Kloss (1918), Robinson *et al.* (1924), Stattersfield *et al.* (1998), Tobias (1995), Wheatley (1996).

#### Genus *HARPACTES* Swainson, 1833

#### 6. Malabar Trogon

##### *Harpactes fasciatus*

**French:** Trogon de Malabar **German:** Malabartrogon **Spanish:** Trogón Malabar  
**Other common names:** Ceylon/Southern Trogon

**Taxonomy.** *Trogon fasciatus* Pennant, 1769, Sri Lanka.

Two subspecies recognized.

**Subspecies and Distribution.**

*H. f. malabaricus* (Gould, 1834) - W & E peninsular India in Western and Eastern Ghats.

*H. f. fasciatus* (Pennant, 1769) - Sri Lanka.

**Descriptive notes.** 29-30 cm; 62-64 g. Male of nominate race has bill and orbital ring blue with rich blue bar of bare skin running under eye from upper mandible; head to mid-breast greyish-black with white breastline, mid-breast to undertail-coverts pinkish-red; upperparts yellowish-brown, wingpanel narrowly barred whitish, uppertail rufous-brown with blackish terminal band. Female has dull brown head and breast, vague buff breastline and tawny-yellow mid-breast to undertail-coverts, wingpanel barred buff. Juvenile male like female, but with greyish head and breast. Race





*malabaricus* slightly larger, male with head and breast sooty-black. VOICE. A throaty, musical "cue-cue-cue-...", like an oriole (*Oriolus*), and low rolling "kr-r-r-r" when alarmed.

**Habitat.** Middle storey of dense primary and secondary broadleaf evergreen, semi-evergreen and moist deciduous forest, preferably with abundance of bamboo, in tropical and subtropical zones at up to 1500 m; recorded also in plantations (e.g. mahogany) in Kerala. Reaches 1800 m in Sri Lanka, where appears to favour the intermediate belt of country between the wet and dry zones.

**Food and Feeding.** Caterpillars, moths, beetles, grasshoppers, cicadas, bugs, stick-insects and other insects; also leaves and berries. Crepuscular, hunting well after sunset. Often trails mixed-species flocks; up to 4 individuals recorded in such flocks.

**Breeding.** Feb-Jun. Nest an unlined natural hollow in or on top of a broken stump, usually less than 6 m from ground, in deep forest. Eggs 2-4. No other information.

**Movements.** Chiefly resident, although in W India considered a local cold-season immigrant (Nov-Mar) around Bombay.

**Status and Conservation.** Not globally threatened. Locally frequent in India, though generally uncommon; widespread throughout Western Ghats; apparently common and widespread in Kerala. Frequent in Sri Lanka in humid forest, infrequent in dry and hill country; Sinharaja Forest Man and Biosphere Reserve is a major stronghold.

**Bibliography.** Abdulali (1972a), Ali (1949, 1969, 1996), Ali & Abdulali (1938), Ali & Ripley (1983), Ali (1935-1937), Baker (1934a), Bourdillon (1878), Chakravathy & Purna Chandra Tejasvi (1992), Daniels (1997), Deraniyagala (1955), Grimmett *et al.* (1998), Harrison (1999), Henry (1998), Hume (1890), Jones *et al.* (1998), Kannan (1998), Kazmierczak (2000), Lamsfuss (1998), Legge (1983), Phillips (1978), Ripley (1982), Saha & Dasgupta (1992), Sashikumar (1996), Sugathan & Varghese (1996), Uttangi (1993), Whistler (1944), Zacharias & Gaston (1999).

## 7. Red-naped Trogon

### *Harpactes kasumba*

French: Trogon à nuque rouge

German: Rotnackentrogon

Spanish: Trogón Kasumba

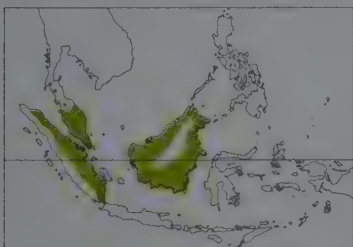
**Taxonomy.** *Trogon Kasumba* Raffles, 1822, Sumatra.

Two subspecies recognized.

**Subspecies and Distribution.**

*H. k. kasumba* (Raffles, 1822) - southernmost peninsular Thailand, Peninsular Malaysia and Sumatra.

*H. k. impavidus* (Chasen & Kloss, 1931) - Borneo.



**Descriptive notes.** 32-34 cm; 72 g. Male nominate race with black head and upper breast, blue bill and orbital ring, red nuchal band meeting broad cobalt-blue facial skin, white breastline; yellowish-brown upperparts and uppertail, latter with black outline, bright red underparts; undertail white on black. Female has dull greyish-brown head and upper breast, vague buffy-whitish breastline and otherwise tawny-yellow underparts. Juvenile similar to female. Race *impavidus* slightly smaller and shorter-winged, but overlap exists. VOICE. Subdued but rather harsh, evenly pitched "kau, kau, kau, kau" of 3-6 notes, lower-pitched and more

spaced than that of *H. diardi*; female gives quiet whirring rattle.

**Habitat.** Middle to upper storeys of chiefly primary but also logged evergreen forest, in lowlands and foothills to 600 m; also peat swamp-forest. In Borneo, penetrates upland and highland dipterocarp forest, lower montane forest (up to 1220 m), streamside vegetation, and even shifting cultivation and cocoa plantations. Recently fledged bird seen in kerangas (impoverished heath forest).

**Food and Feeding.** Poorly known. One stomach held spiders, others stick-insects. Often associates with mixed-species flocks.

**Breeding.** Nest in Peninsular Malaysia in Jul; females in breeding condition in Feb and May; recently fledged bird in Jun in Borneo. One nest in cavity 1-2 m up tree stump by forest path; 2 eggs. No further information available.

**Movements.** Apparently sedentary.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Rare and now threatened by habitat loss in peninsular Thailand, where known for certain from only a single area, which is protected. Fairly common in lowlands in S Peninsular Malaysia; became extinct in Singapore some time after 1940. Relatively few records from Sumatra, but may be locally fairly common; present in Bukit Barisan Selatan National Park and scarce in Way Kambas National Park. Rather scarce in Sarawak, but occurs at up to 600 m; present in Similajau National Park. Uncommon in Tanjung Puting National Park, Kalimantan.

**Bibliography.** Andrew (1992), Davies & Payne (1982), Davison (1995), Duckworth *et al.* (1997), Gore (1968), Harrison & Hartley (1934), Jeyarajasingam & Pearson (1999), Johns (1983, 1986a, 1989), Lekagul & Round (1991), Lim Kim Seng (1992), MacKinnon & Philipps (1993), van Marle & Voous (1988), Medway & Wells (1976), Nash & Nash (1988), Parrott & Andrew (1996), Riley (1938), Robson (2000a), Round (1988), Smythies (1999), Thompson (1966), Vowles & Vowles (1984), Wells (1984, 1999), Wilkinson, Dutton & Sheldon (1991).

## 8. Diard's Trogon

### *Harpactes diardii*

French: Trogon de Diard

German: Diardtrogon

Spanish: Trogón de Diard

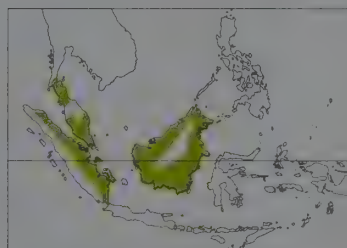
**Taxonomy.** *Trogon diardii* Temminck, 1832, Pontianak district, Borneo.

May form a superspecies with *H. ardens*. Two subspecies recognized.

**Subspecies and Distribution.**

*H. d. sumatranus* A. W. H. Blasius, 1896 - S peninsular Thailand, Peninsular Malaysia, Lingga Archipelago and Sumatra.

*H. d. diardii* (Temminck, 1832) - Bangka I (off E Sumatra) and Borneo.



**Descriptive notes.** 34 cm; 101 g. Male nominate race with black head and upper breast, purplish-blue orbital ring, maroon-washed mid-crown to hindcrown, strong pink hind-collar, and pale pink breastline; pale brown upperparts and uppertail, scarlet belly and vent, with blackish vermiculations on white (looks grey) undertail. Female has drab brownish head and upper breast; has rosier pinkish-red lower underparts than male. Juvenile resembles female. Race *sumatranus* has maroon of head in male generally confined to nape, though this is also the case in some Bornean birds. VOICE. A cadence of 10-12

"kau" notes, the second rather higher than the first and remainder falling, with last few notes usually slightly lower.

**Habitat.** Middle and lower storeys of primary and logged forest in lowlands and hills, to 900 m in Peninsular Malaysia, in Thailand rarely to 600 m. In Borneo, lowland, upland and highland dipterocarp forest, logged dipterocarp forest, streamside vegetation, kerangas (impoverished heath forest), and sometimes in cocoa plantations near secondary forest, to 1200 m but probably usually much lower. Peat swamp-forest in Brunei and Sumatra.

**Food and Feeding.** Caterpillars, beetles, stick-insects, locustids and other Orthoptera, and fruits (including *Ficus pellucido-punctata*).

**Breeding.** Feb to mid-May in Peninsular Malaysia; mid-May to Aug, probably Sept, in Borneo, but birds in breeding condition also in Feb and Apr. Nest a cavity 1-3 m up in dead tree or stump. No further information.

**Movements.** Apparently sedentary.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Generally uncommon and now threatened by habitat loss in peninsular Thailand, where known for certain from four protected areas. Fairly common in S Peninsular Malaysia, where 2 pairs in one 15-ha plot; became extinct in Singapore some time after 1940. Fairly common throughout Borneo; most numerous trogon at Cocoa Research Station in Sabah, present in Similajau National Park in Sarawak, and uncommon in Tanjung Puting National Park in Kalimantan. In Sumatra, present in Bukit Barisan Selatan National Park and Berbak Game Reserve, rare in Way Kambas National Park.

**Bibliography.** Andrew (1992), Davies & Payne (1982), Davison (1995), Duckworth *et al.* (1997), Gore (1968), Jeyarajasingam & Pearson (1999), Johns (1989), Lekagul & Round (1991), Lim Kim Seng (1992), MacKinnon & Philipps (1993), van Marle & Voous (1988), McClure (1998), Medway & Wells (1976), Mees (1986), Müller (1999), Nash & Nash (1988), Parrott & Andrew (1996), Riley (1938), Robson (2000a), Round (1988), Smythies (1999), Thompson (1966), Vowles & Vowles (1984), Wells (1990, 1999), Wilkinson, Dutton & Sheldon (1991).





## 9. Philippine Trogon

### *Harpactes ardens*

French: Trogon des Philippines German: Philippintrogon Spanish: Trogón Filipino

**Taxonomy.** *Trogon ardens* Temminck, 1826, Mindanao.

May form a superspecies with *H. diardi*. Five subspecies recognized.

#### Subspecies and Distribution.

*H. a. herberti* Parkes, 1970 - NE Luzon.

*H. a. luzoniensis* Rand & Rabor, 1952 - Luzon (except NE), Marinduque and Catanduanes.

*H. a. minor* Manuel, 1958 - Polillo.

*H. a. lineae* Rand & Rabor, 1959 - Samar, Biliran, Leyte and Bohol.

*H. a. ardens* (Temminck, 1826) - Dinagat, Mindanao and Basilan.



**Descriptive notes.** 29-30 cm; 82-114 g. Male nominate race has bill yellow with bright green base, head and throat black with violet-blue facial skin, crown suffused maroon; neck and mantle pale brown, rump lighter; tail rufous with blackish terminal band; breast greyish-pink, breastline bright red, rest of underparts pinkish-red. Female like male above but duller, head and throat brownish-black, breast and belly orange-brown, barring on wingpanel rich brown; bill and facial skin as male. Juvenile resembles female, but with coarse barring on wingpanel. Race *lineae* has more extensive and indistinct throat patch than any other, larger

bill; *luzoniensis* has slightly shorter bill, and duller upperparts, male without maroon wash on crown; *minor* small, with red colours darker; *herberti* with maroon wash over entire crown, slightly larger bill than *luzoniensis*. **Voice.** Descending series of soft notes.

**Habitat.** Lower and middle strata of primary forest of all types (including on ultrabasic rock) except mossy forest, occasionally also in second growth; up to 1670 m, but commoner at lower elevations, 200-600 m, often in dense vegetation in valleys and along streams. On Mt Isarog, in Luzon, found near transition between dipterocarp and lower montane forest at 900 m, but records 450-1060 m. On Dinagat, occurs in darker parts (third-storey trees) of original dipterocarp forest areas and remnant patches growing in small valleys and on lower hill slopes.

**Food and Feeding.** Grasshoppers recorded. On Mindanao, a bird in flight seen plucking a 20-cm stick-insect off a branch, then flying off to eat it nearby.

**Breeding.** Mar-May: nestlings and juveniles in Apr-Jun. Nest in hole in tree; 1 located 6 m up in dead tree. Eggs 3. No other information.

**Movements.** Apparently resident, although some altitudinal movements may occur.

**Status and Conservation.** Not globally threatened. May have declined substantially since 19th century, when said by explorers to be abundant from Luzon to Basilan, whereas today it is very common only locally (e.g. in parts of Sierra Madre of Luzon), otherwise no more than fairly common; very uncommon in Bataan, Luzon, in 1948. Uncommon and very local in 1970's on Marinduque. Species is apparently trapped on Bohol, for unstated reasons, but not uncommon within Rajah Sikatuna National Park. Fairly common in 1972 on Dinagat. Sibulan, in S Polillo, appears to be the only site where race *minor* survives, although it had been assumed to occur on other islands in the group; this subspecies therefore presumably highly threatened.

**Bibliography.** Brooks, Dutson, Gabutero & Timmins (1995), Brooks, Dutson, King & Magsalay (1996), Danielsen *et al.* (1994), Dickinson *et al.* (1991), Gilliard (1950a), Gonzales (1983), Gonzales & Rees (1988), Gonzalez (1997), Goodman & Gonzales (1990), Kennedy *et al.* (2000), Kutter (1883), Manuel (1957), McGregor (1909-1910), Parkes (1970), duPont (1971), duPont & Rabor (1973b), Rabor (1955, 1977), Rand & Rabor (1960), Robson & Davidson (1996).

## 10. Whitehead's Trogon

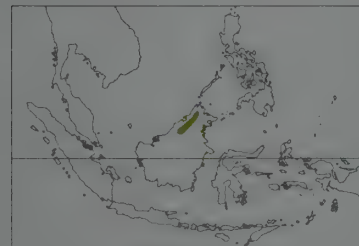
### *Harpactes whiteheadi*

French: Trogon de Whitehead German: Graubrusttrogon Spanish: Trogón de Borneo

**Taxonomy.** *Harpactes whiteheadi* Sharpe, 1888, Kinabalu, Borneo.

Monotypic.

**Distribution.** Spinal range of N Borneo from Kinabalu to Mt Dulit, including Mt Lunjut (Kalimantan).



**Descriptive notes.** 29-31 cm. Male has red head, blue bill and orbital ring, black throat, grey breast, and red belly; pale rich brown upperparts; largely white undertail. Female like male, but with red replaced by ochre-brown to cinnamon, barring on wingpanel pale brown. **Voice.** Song up to 5 even-pitched whistles, "poop poop poop poop"; soft rolling "rrrr" notes, sometimes followed by loud "kekekeke", dropping in pitch; a peculiar growling note heard from a hunting bird at close range was presumably the same as the "rrrr" notes.

**Habitat.** Montane forest and sparse moss forest at 900-1500 m; frequents the dark, wet patches of old forest, generally perching in the higher branches of the understorey.

**Food and Feeding.** Grasshoppers, locustids, ants, large green leaf-insects and stick-insects. Stones also found in stomach.

**Breeding.** Female in breeding condition in Mar; family party of 3 in Jul. Nest not certainly known: a used trogon nest, with female of this species nearby, was found 1-8 m up in a rotten stump 3 m tall in late Apr. Eggs, incubation and nestling periods, and other breeding details undescribed.

**Movements.** Apparently sedentary.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Restricted-range species; present in Bornean Mountains EBA. Appears to be uncommon throughout its limited though relatively secure range; reputedly declining on Mt Kinabalu, although still very poorly known and full vocabulary not known.

**Bibliography.** van Balen (1997), Banks (1937), Davison (1992), Holmes (1997), Inskipp *et al.* (1996), MacKinnon & Phillips (1993), Pope (1997), Robson (1996b), Sharpe & Whitehead (1890), Smythies (1999), Stattersfield *et al.* (1998), Sujatnika *et al.* (1995), Wheatley (1996).

## 11. Cinnamon-rumped Trogon

### *Harpactes orrhophaeus*

French: Trogon canelle German: Zimtbürltrogon Spanish: Trogón Canela

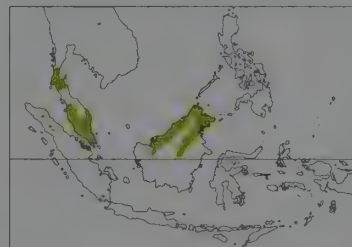
**Taxonomy.** *Pyrotrogon orrhophaeus* Cabanis and Heine, 1863, Malacca.

Present species and *H. duvaucelii* have sometimes been placed in a separate genus, *Duvaucelius*. Species name sometimes misspelt *orrhophaeus*. Two subspecies recognized.

#### Subspecies and Distribution.

*H. o. orrhophaeus* (Cabanis & Heine, 1863) - peninsular Thailand, Peninsular Malaysia and Sumatra.

*H. o. vidua* Ogilvie-Grant, 1892 - N & C Borneo.



**Descriptive notes.** 25 cm; 45-61 g. Male of nominate race has black hood, blue bill, eyebrow and narrow orbital ring, pale brown upperparts and uppertail; pinkish-red underparts; undertail white with black border. Differs from extremely similar *H. duvaucelii* in slightly larger size, slightly larger bill, pinker underparts, and lack of red rump. Female with dark brown head with chestnut on lores and around eye; rump and underparts rusty-buff to yellowish-buff. Juvenile resembles female. Race *vidua* barely distinct, but barring on wingpanel less dense, breast buffier; female darker above, more chestnut on face and throat,

barring on wingpanel stronger. **Voice.** Song 3-4 falling "ta-aup" notes; harsh explosive "purrr".

**Habitat.** Middle and lower storeys of forest in the lowlands and hills, to 180 m in Peninsular Malaysia and to 140 m in Thailand; often in the shrub layer only 2-4 m up. In Borneo considered a slope specialist, occurring in submontane zone, chiefly at 1000-1400 m, although also recorded in lowlands, in tall primary but also logged dipterocarp forest; recorded from peat-swamp-forest in Brunei.

**Food and Feeding.** Stick-insects and leaf-insects recorded in stomachs. Still-hunts in fairly dense understorey, 2-3 m up. Has been seen in a mixed-species flock.

**Breeding.** Mar-Apr and Jun in Peninsular Malaysia; in Borneo, male and female in breeding condition in Mar. Nest in cavity 1-1.5 m up in rotten stump in forest. Eggs 2. No other details available.

**Movements.** Apparently sedentary.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Rare and local resident in peninsular Thailand, where now threatened by habitat loss and known from only three protected areas. Formerly judged rare in Peninsular Malaysia, but results of mist-netting now suggest that it may be commonest trogon, though very unobtrusive and shy; specialization on plains-level closed-canopy forest, however, means that in a few years it will almost certainly be confined to a small number of protected areas, notably Taman Negara. Rare in Kalimantan, and apparently absent from many areas. In Sumatra, scarce in Way Kambas National Park, and very few other records.

**Bibliography.** Andrew (1992), de Beaufort & de Bussy (1919), Davies & Payne (1982), Duckworth *et al.* (1997), Gore (1968), Jeyarajasingam & Pearson (1999), Johns (1989), Lekagul & Round (1991), MacKinnon & Phillips (1993), van Marle & Voous (1988), McClure (1998), Medway & Wells (1976), Parrott & Andrew (1996), Riley (1938), Robson (2000a), Round (1988), Smythies (1999), Wells (1985, 1990, 1999), Wilkinson, Dutson & Sheldon (1991), Wilkinson, Dutson, Sheldon, Noor & Noor (1991).

## 12. Scarlet-rumped Trogon

### *Harpactes duvaucelii*

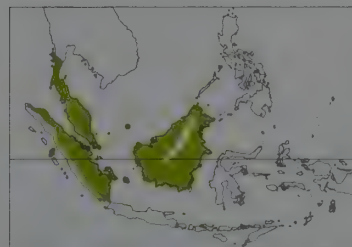
French: Trogon de Duvaucel German: Rotbürltrogon Spanish: Trogón Culirrojo

**Other common names:** Red-rumped Trogon

**Taxonomy.** *Trogon duvaucelii* Temminck, 1824, Sumatra.

This species and *H. orrhophaeus* have sometimes been placed in a separate genus, *Duvaucelius*. Monotypic.

**Distribution.** S Myanmar (S Tenasserim), S Thailand, Peninsular Malaysia, Riau Archipelago, Sumatra, Batu Is, Bangka, Belitung, and Borneo (including Natuna Is).



**Descriptive notes.** 23-24 cm; 34-43 g. Male has black hood with blue bill, eyebrow and narrow orbital ring; rich buff to yellowish-brown upperparts and uppertail, scarlet rump, uppertail-coverts and underparts; undertail white with black bordering. Female has dull brown head and throat, paler buffy-brown breast, reddish-pink belly, and pinkish rump and uppertail-coverts. Juvenile like female but without pink tones, rump and uppertail-coverts more rufous-tinged. **Voice.** Call a very soft, rapid cadence of c. 12 notes, "yau-yau-yau...", accelerating, diminishing, in alarm, a quiet whirring "kir-r-r-r".

**Habitat.** Chiefly middle but also lower storeys and borders of semi-evergreen and evergreen forest, including swamp-forest, in lowlands and hills, to 1070 m in Peninsular Malaysia, but only occasionally to 400 m in Thailand. Lowland, upland and highland dipterocarp forest, and tree plantations, in Sabah, with one sighting as high as 1500 m on Mt Kinabalu. Primary and secondary forest,

riverine forest, old rubber plantations, mangroves and kerangas (impoverished heath forest) in Brunei. Streamside secondary vegetation, high lowland dipterocarp forest, poor-quality highland dipterocarp forest and lower montane forest, at 120-900 m, in C Kalimantan. In Sumatra, also freshwater swamp-forest.

**Food and Feeding.** Green Orthoptera, stick-insects, bugs, beetles, moths and caterpillars (in one case a nymphalid). Several observations of bird on edge of a cleared area sallying out over scrub like a shrike (*Lanius*). Often in mixed-species flocks.

**Breeding.** Feb-Jun; Mar and May in Peninsular Malaysia. Only documented nest was 1-6 m up in a rotten stump 2-5 m tall. Eggs 2. No further information available.

**Movements.** No evidence of movements; suggestion of local migrations in Bahau area of Borneo was based on increased calling activity.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Generally uncommon and now threatened by habitat loss in peninsular Thailand, where known from six protected areas. Fairly common in S Peninsular Malaysia. Common throughout lowland Borneo, and is the commonest trogon in Barito Ulu area of Kalimantan; present in Similajau National Park in Sarawak; uncommon to common in Tanjung Puting National Park in Kalimantan. Considered the most numerous lowland trogon in Sumatra; present in Berbak Game Reserve and Bukit Barisan Selatan National Park, and frequent in Way Kambas National Park.

**Bibliography.** Andrew (1992), Chasen & Hoogerwerf (1941), Davies & Payne (1982), Davison (1995), Duckworth *et al.* (1997), Gore (1968), Holmes (1994), Jeyarajasingam & Pearson (1999), Johns (1989), Lekagul & Round (1991), MacKinnon & Phillips (1993), Mann (1987, 1988), van Marle & Voous (1988), McClure (1998), Medway & Wells (1976), Nash & Nash (1988), Parrott & Andrew (1996), Riley (1938), Robinson & Kloss (1918), Robinson *et al.* (1924), Robson (2000a), Round (1988), Rutgers & Norris (1977), Smythies (1986, 1999), Thompson (1966), Vowles & Vowles (1984), Wells (1999), Wilkinson, Dutson & Sheldon (1991).

## 13. Orange-breasted Trogon

### *Harpactes oreskios*

**French:** Trogon à poitrine jaune **German:** Orangebrusttrogon **Spanish:** Trogón Pechinaranja

**Taxonomy.** *Harpactes oreskios* Temminck, 1823, Java.

Populations from S Myanmar across to S Indochina sometimes separated as race *stellae*, but probably indistinguishable from *uniformis*. Four subspecies normally recognized.

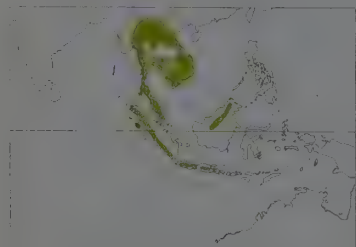
**Subspecies and Distribution.**

*H. o. uniformis* (Robinson, 1917) - E & S Myanmar, SW China (S Yunnan) and Vietnam S to Sumatra.

*H. o. nias* Meyer de Schauensee & Ripley, 1940 - Nias I (off NW Sumatra).

*H. o. oreskios* Temminck, 1823 - Java.

*H. o. dultensis* Ogilvie-Grant, 1892 - NW Borneo.



**Descriptive notes.** 25-26 cm; 57 g. Male nominate race with dull olive-yellowish head with blue orbital ring, rufous-chestnut upperparts and uppertail with paler rump, bold broad white bars on wingpanel, yellow (grey-based) upper breast with vague white mid-line, orange lower breast becoming paler on vent; white on black undertail. Female has more grey-brown head and upperparts shading to pale buffy-brown rump, grey breast, yellow lower underparts. Juvenile similar to female, male with warmer brown upperparts. Race *uniformis* lacks paler rump, has olive-yellow upper breast, latter greyer in female; *nias* has somewhat darker crown and larger bill than *uniformis*; *dultensis* like *uniformis* but much smaller, and with greener breast. **VOICE.** A phrase of 3-4 even-pitched notes, "tau-tau-tau", with introduction of 1-3 notes, "to (to to)". In Borneo a repeated "kek kek", presumably same as a barking call heard on Nias.

**Habitat.** Inhabits mid-stratum and lower canopy of primary semi-evergreen and lowland and lower montane evergreen forest and swamp-forest, but also disturbed tracts with much bamboo, thin tree jungle, open dry forest, mixed deciduous forest, bamboo forest, and even clumps of trees near forest tracts; occurs in lowlands up to 1100 m in Thailand; up to 1300 m in Peninsular Malaysia; at 300-1500 m (apparently mainly 800-1000 m) in Borneo and Sumatra; and up to 1200 m in Java. Occurs low down in heavy secondary jungle, often in substage growth, on Nias. Little use of degraded forest in Laos.

**Food and Feeding.** Diet includes Orthoptera, cicadas, bugs, beetles (including Tenebrionidae), ants, stick-insects and their larvae, caterpillars; also spiders, lizards, fruit, and regularly an admixture of vegetable material. Appears to feed more frequently on the ground than other trogons, although others report that feeding station in forest is higher than that of *H. kasumba*. Recorded following mixed-species flocks.

**Breeding.** Feb-Apr in Myanmar, Mar in Thailand; Jan-May in Peninsular Malaysia, where half-grown bird seen in Feb on Langkawi; early months of year (presumably Jan-Mar) in Kelabit uplands in Sarawak; Feb, May, Jun and Oct in Java. Nest in hollow stump, sometimes in dead bamboo, often less than 1 m from ground, commonly under 2 m; once 4 m up in hollow in dead branch of a "zimbom" tree. Eggs generally 2-3, but 1-4 recorded. No information available on incubation and nestling periods.

**Movements.** Apparently sedentary.

**Status and Conservation.** Not globally threatened. Rare in Yunnan; in Myanmar, common in Tenasserim but scarcer elsewhere; common in Thailand, including in Doi Suthep-Pui National Park, and the commonest trogon in the peninsula; moderately common in some areas in Laos, and present in several major existing or proposed "national biodiversity conservation areas"; present in Nam Bai Cat Tien National Park in Vietnam; fairly common in N & C Peninsular Malaysia. In Borneo, not common on Kinabalu but the common trogon of the Kelabit uplands above 900 m; common at submontane site in Barito Ulu area of Kalimantan in 1989. Only a single record during c.1940-1985 in Sumatra, but in more recent times present in Bukit Barisan Selatan and Gunung Leuser National Parks; uncommon in Java.

**Bibliography.** Baker (1934a), Bingham (1877), Chasen & Hoogerwerf (1941), Cheng Tsohsin (1987), Davies & Payne (1982), Deignan (1945), Delacour & Jabouille (1931), Duckworth (1996), Duckworth *et al.* (1999), Evans & Timmins (1998), Glenister (1971), Gore (1968), Hellebrekers & Hoogerwerf (1967), Holmes (1994), Hume (1890), Jeyarajasingam & Pearson (1999), Johns (1989), Lekagul & Round (1991), MacKinnon (1988), MacKinnon & Phillips (1993, 2000), van Marle & Voous (1988), McClure (1974), Medway & Wells (1976), Meyer de Schauensee (1946), Riley (1938), Ripley (1944), Robinson *et al.* (1924), Robson (2000a), Round (1984), Sharpe & Whitehead (1890), Smythies (1986, 1999), Stepanyan (1995), Thewlis *et al.* (1996), Vo Quy (1975), Wang Sung

(1998), Wells (1999), Wilkinson, Dutson & Sheldon (1991), Wilkinson, Dutson, Sheldon, Noor & Noor (1991), Yang Lan *et al.* (1995), Zhao Zhengjie (1995).

## 14. Red-headed Trogon

### *Harpactes erythrocephalus*

**French:** Trogon à tête rouge **German:** Rotkopftrogon **Spanish:** Trogón Cabecirrojo

**Taxonomy.** *Trogon erythrocephalus* Gould, 1834, Rangoon.

Birds from NE India to N Myanmar sometimes separated as race *hodgsoni*, but differences from nominate race and *helenae* not constant. Ten subspecies currently recognized.

**Subspecies and Distribution.**

*H. e. erythrocephalus* (Gould, 1834) - Himalayas from Nepal through NE India to Myanmar and W Thailand.

*H. e. helenae* Mayr, 1941 - N Myanmar and S China (W Yunnan).

*H. e. yamakanensis* Rickett, 1899 - SE China (SE Sichuan E to Fujian).

*H. e. rosa* (Stresemann, 1929) - Guangxi (Yao Shan).

*H. e. intermedius* (Kinnear, 1925) - SE Yunnan, Tonkin, N Annam and N Laos.

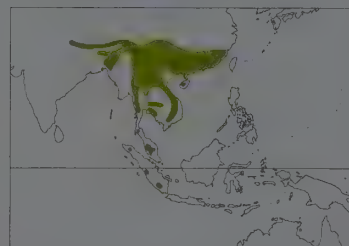
*H. e. hainanus* Ogilvie-Grant, 1900 - Hainan I.

*H. e. annamensis* (Robinson & Kloss, 1919) - NE Thailand, S Laos, S Annam and Cochinchina.

*H. e. klossi* (Robinson, 1915) - Bantat Range in W Cambodia and extreme E Thailand, also hills on Koh Chang I (SE Thailand).

*H. e. chaseni* Riley, 1934 - Malay Peninsula.

*H. e. flagrans* (S. Müller, 1835) - Sumatra.



**Descriptive notes.** 31-35 cm; 75-110 g. Male nominate race with blue bill tipped blackish, purplish-blue orbital ring; head and nape to mid-breast dull crimson with white breastline, mid-breast to vent pinkish-red; upperparts and uppertail rufescent-brown. Female has crimson areas replaced with brown. Juvenile like female, but buffish-white on lower breast, belly and flanks. Race *helenae* largest, with strong red belly; *yamakanensis* large, darker around head, with paler pink belly and more black in tail, male with cinnamon band across lower breast, female with darker brown head and upper neck; *rosa* female paler above and below than *yamakanensis*; *hainanus* like nominate but smaller, with much less red on head; *intermedius* smaller, paler above but darker below than *rosa*, with paler cadmium-red on head and belly, generally darker than *annamensis*, female intermediate between those of nominate and *yamakanensis*; *annamensis* smaller and more ochraceous above than nominate, with little red on head; *klossi* brighter than *annamensis*; *chaseni* a shade darker above than *klossi*, wingpanel with finer barring than *annamensis*; *flagrans* almost exactly like nominate, but considerably smaller. **VOICE.** Song 5 or more well-spaced mellow notes, like those of an oriole (*Oriolus*), in descending sequence, "tyaup, tyaup, tyaup, tyaup, tyaup..."; alarm a chattering croak, "tewirr".

**Habitat.** Exclusively forest: middle storey and lower canopy of dense broadleaf lower and upper montane evergreen forest and mixed bamboo, preferring interior of damp, dark evergreen cover and cool ravines. Essentially hardwood and bamboo forest in S China. Little use made of degraded forest in Laos. Mainly 250-1000 m in Nepal; up to 1800 m and even 2400 m in India; 245-2090 m in Bhutan; to 2000 m in Thailand; 600-1500 m in China, where commonest at 700-900 m, although a recent record from as high as 2500 m in Yunnan; 300-900 m in Peninsular Malaysia, but no records below 700 m in S; 500-1900 m in Sumatra.

**Food and Feeding.** Green Orthoptera, stick-insects, cicadas, millipedes, flies, beetles, centipedes, woodlice; also leaves (notably bamboo) and berries, with "strong-smelling seeds" in stomachs. Hawks moths in early morning and evening.

**Breeding.** Apr in China; Apr-Aug, chiefly May-Jun, in India; Mar-May in Myanmar; Mar-Apr in Thailand; juveniles in Mar and May in Peninsular Malaysia. Nest an unlined hollow in rotten tree trunk or old woodpecker hole, 1-5-5 m up, in deep forest, but sometimes by a track or stream. Eggs 2-4. Incubation and nestling periods undocumented.

**Movements.** Apparently sedentary for the most part; may perform altitudinal movements in S Laos. **Status and Conservation.** Not globally threatened. Fairly common to uncommon in China. Now local and very uncommon in Nepal, probably as result of habitat loss; in India, locally fairly common in NE but uncommon elsewhere; frequent in Bhutan; local in Bangladesh. Common throughout Myanmar, including race *helenae* at 2100 m on Yunnan border; common in Thailand, including in Doi Suthep-Pui and Khao Yai National Parks; fairly common in Peninsular Malaysia; moderately common in some areas in Laos, and present in several major existing or proposed "national biodiversity conservation areas"; present in Bach Ma, Nam Bai Cat Tien, Tam Dao and Cuc Phuong National Parks in Vietnam. Rather rare in Sumatra, where apparently only 1 record in period 1930-1985.

**Bibliography.** Ali & Ripley (1983), Ali *et al.* (1996), Baker (1934a), Biswas (1959), Caldwell & Caldwell (1931), Cheng Tsohsin (1987), Deignan (1945), Delacour & Jabouille (1931), Duckworth (1996), Duckworth *et al.* (1999), Échécopar & Hùe (1978), Evans & Timmins (1998), Evans *et al.* (2000), Glenister (1971), Grimmett *et al.* (1998), Guan Guanxun (1986), Harvey (1990), Hume (1890), Inskipp & Inskipp (1991), Jeyarajasingam & Pearson (1999), Lekagul & Round (1991), MacKinnon & Phillips (1993, 2000), van Marle & Voous (1988), McClure (1974), Medway & Wells (1976), Peng Yanzhang *et al.* (1980), Riley (1938), Ripley (1982), Robson (2000a), Robson *et al.* (1993a), Round (1984), Smythies (1986), Stanford & Mayr (1941), Stepanyan (1995), Thewlis *et al.* (1996), Vo Quy (1975), Wang Sung (1998), Wells (1999), Wells & Medway (1976), Yang Lan *et al.* (1995), Yen (1933), Zhao Zhengjie (1995).

## 15. Ward's Trogon

### *Harpactes wardi*

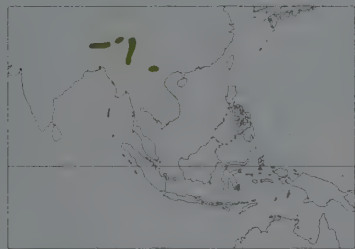
**French:** Trogon de Ward **German:** Rosenschwanztrogon **Spanish:** Trogón de Ward

**Taxonomy.** *Pyrotrogon wardi* Kinnear, 1927, Seinghku Valley, 8000 feet [c. 2500 m], Myanmar. Monotypic.

**Distribution.** Bhutan and NE India through N & E Myanmar to SC China (W Yunnan) and N Vietnam (Tonkin).

**Descriptive notes.** 35-38 cm; 115-120 g. Male with bill deep pink, orbital ring pale blue; head, breast and upperparts slate with maroon wash, with reddish-pink forehead and supercilium, underparts and outer tail, rest of uppertail slaty. Female has bill yellow with black culmen; brownish-



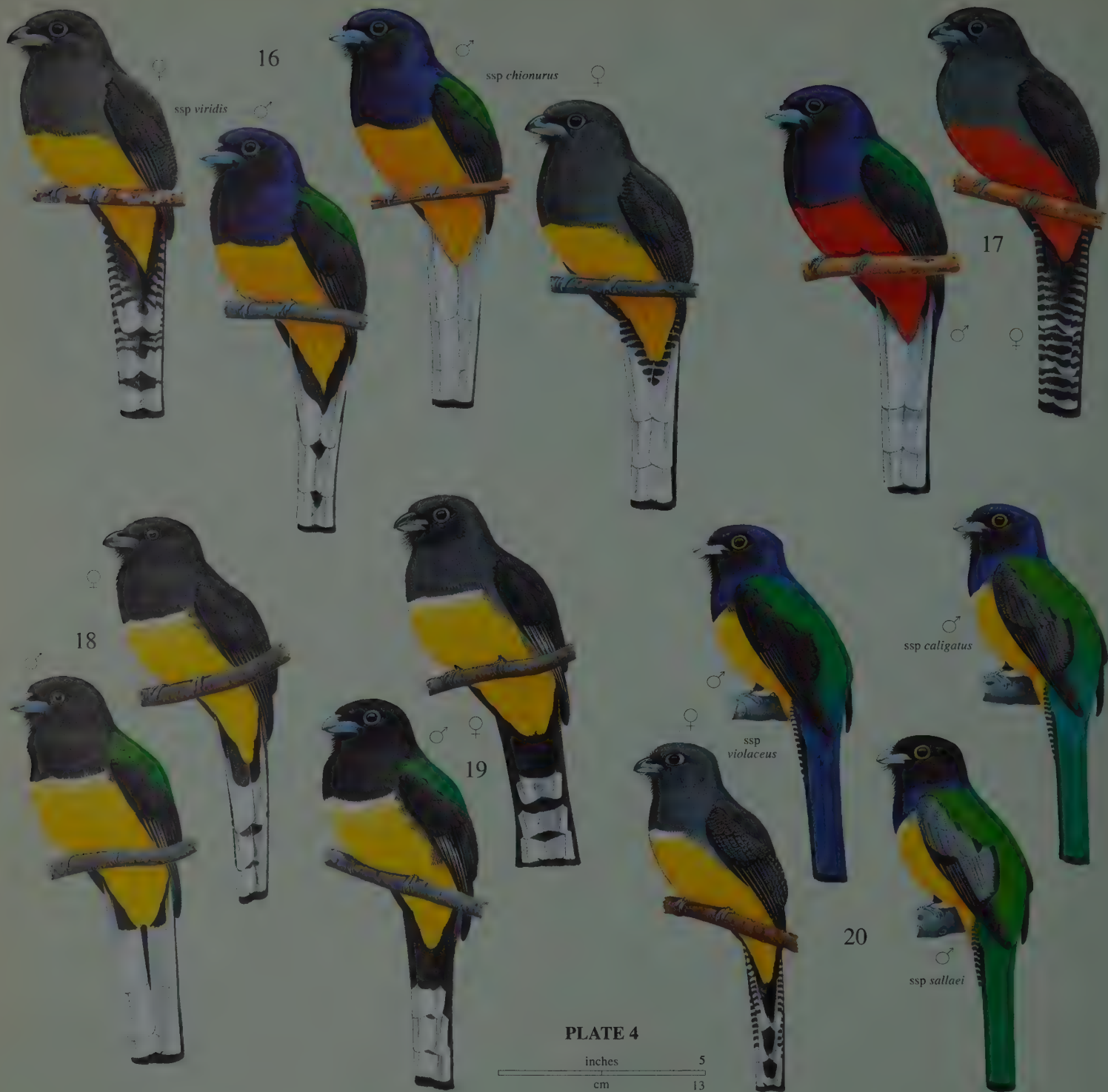


stick-insects, grasshoppers and bugs; species also takes berries. Large seeds (probably acorns) found in stomach of 1 specimen. Stomachs from Indochina held only insects, most of them large ones.

maroon areas replaced with dark olive and pink areas with yellow. Juvenile male apparently undescribed, female warmer above than adult female and with less yellow on forehead. Voice. A series of rapid mellow “klew” notes, often slightly accelerating and dropping in pitch; call a harsh “whirrur”.  
**Habitat.** Inhabits lower storey, undergrowth and bamboo in tall subtropical hill forest of *Quercus*, *Castanopsis*, etc., and temperate broadleaf evergreen forest, often with creepers and vines; normally at 1500-3200 m, but occasionally down to 300 m.

**Food and Feeding.** Insects such as moths, stick-insects, grasshoppers and bugs; species also takes berries. Large seeds (probably acorns) found in stomach of 1 specimen. Stomachs from Indochina held only insects, most of them large ones.

**Breeding.** Birds in breeding condition in late Mar and early Apr. No further information available, and nest unrecorded.  
**Movements.** Apparently moves to lower elevations in winter.  
**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Restricted-range species; present in Eastern Himalayas EBA and the Fan Si Pan and Northern Laos Secondary Area. Classed as Vulnerable in 1994, but in Bhutan populations have now been located that appear fairly secure, at least for present. Widely, if sparsely, distributed in Bhutan; regularly recorded in small numbers in Thrumshingla National Park. Rare and local in India; very rare in Yunnan; scarce to uncommon in N Myanmar, although common, at least formerly, in mountains NE of Myitkyina at 2400-2700 m. Said to have been common in 1939 on Fan Si Pan, in Vietnam, at 1500-2300 m, but no recent data from this area.  
**Bibliography.** Ali & Ripley (1983), Ali *et al.* (1996), Bishop (1999a), Cheng Tsohsin (1987), Collar *et al.* (1994), Crosby (1996), Delacour & Jabouille (1931), Eames & Ericson (1996), Grammett *et al.* (1998), Inskipp *et al.* (2000), Kazmierczak (2000), MacKinnon & Philipps (2000), Peng Yanzhang *et al.* (1980), Ripley (1982), Robson (1996a, 2000a), Smythies (1986), Stanford & Mayr (1941), Stattersfield *et al.* (1998), Tymstra *et al.* (1996), Vo Quy (1975), Yang Lan *et al.* (1995), Zhao Zhengjie (1995).



## PLATE 4

## Family TROGONIDAE (TROGONS) SPECIES ACCOUNTS

### Subfamily TROGONINAE

### Genus *TROGON* Brisson, 1760

#### 16. White-tailed Trogon

##### *Trogon viridis*

**French:** Trogon à queue blanche **German:** Weißschwanztrogon **Spanish:** Trogón Coliblanco

**Other common names:** Green-backed Trogon

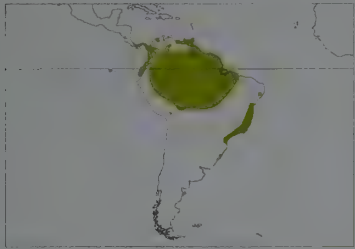
**Taxonomy.** *Trogon viridis* Linnaeus, 1766, Cayenne.

Forms a superspecies with *T. bairdii*, *T. citreolus* and *T. melanocephalus*; sometimes considered conspecific with *T. bairdii*, from which race *chionurus* differs mainly in belly colour and female's undertail pattern, with habits and vocalizations rather similar. DNA studies suggest present species may actually be closer to *T. violaceus* and *T. curucui*. Race *chionurus* sometimes considered a distinct species. Birds from SE Brazil described as race *melanopterus*, but individual variation, as well as overlap in biometrics with populations elsewhere in species' range, render separation doubtful. Species commonly, but incorrectly, treated under the name *T. strigilatus*; this name was applied to female in same publication as, and just before, first use of *viridis*, but it was subsequently dropped in favour of present name on principle of first reviser. Two subspecies recognized.



Subspecies and Distribution.

*T. v. chionurus* P. L. Selater & Salvin, 1871 - Atlantic slope of W Panama through Canal Zone (whence on both slopes) to Colombia W of E Andes, and W Ecuador.  
*T. v. viridis* Linnaeus, 1766 - E of Andes from Colombia S to Peru and N Bolivia, and E to the Guianas, Trinidad and E Brazil (Maranhão, N Mato Grosso, Alagoas, and Bahia to São Paulo).



*chionurus* with rich blue on mantle and rump, more extensive white on undertail. VOICE. Song a series of up to 16 brisk “kyoh” or “cow” notes, usually accelerating (race *viridis*) or not (*chionurus*), and becoming louder near end, sometimes with rallentando; also low purr and single “chuck”.

**Habitat.** Usually found in canopy and subcanopy of humid and wet lowland and foothill forest, forest edge, clearings, plantations, second-growth woodland, gallery forest and, notably, younger growth; in Colombia, occurs up to 1000 m in areas W of Andes and up to 1200 m to E of Andes; in Venezuela, up to 800 m N of R Orinoco and up to 1300 m S of it. In Surinam occupies forested sand ridges and coffee plantations on coast, also occurring in savanna forest as well as interior forest; although absent from high mangroves (*Avicennia*) in Surinam, in neighbouring French Guiana enters swamp-forest and old mangroves. In Brazil, humid or dry forest in both lowlands and mountains; in Serra do Mar sometimes occurs alongside *T. surrucura* and *T. rufus*. Prefers interior of transition forest and swamp-forest in W Amazonia. Increases in numbers in logged forest.

**Food and Feeding.** Fruits and berries, including Myrtaceae and Anonaceae; also beetles (lampyrids), Orthoptera (including grasshoppers), large green caterpillars and other lepidopteran larvae, large ants, stick-insects, lizards (teids). Joins mixed-species flocks.

**Breeding.** Individuals in breeding condition in Mar-Jul in Panama and in Feb-Apr in Venezuela; Jan-Jun in Colombia; Feb-Jul in Surinam, but pairs seen excavating in Aug and at nest in Dec; Mar, May and Jul in Trinidad; Aug-Sept and Dec-Mar in French Guiana; Jan and Mar in Brazil, with copulation mid-Sept in S Brazil. Nest in arboreal termitarium, sometimes in tree hole (at least in Trinidad), often in quite open situation at edge of forest clearing, but commonly 10-20 m from ground, and recorded as low as 2 m. Eggs 2-3. Incubation and fledging periods unrecorded.

**Movements.** Apparently sedentary.

**Status and Conservation.** Not globally threatened. Locally fairly common, including on Barro Colorado I, Panama, but seemingly rare in E Panamá Province. Common in Colombia, where along with *T. melanurus* the most numerous trogon E of Andes; race *chionurus* common in NW Colombia; common in Las Orquídeas National Park but uncommon in Munchique National Park. In Surinam the commonest trogon in coastal region; in French Guiana, S Venezuela and adjacent N Brazil the commonest trogon anywhere; common in Trinidad. Common in tropical lowlands in Peru, but less so above 750 m (N Peru); common at Tambopata. Present in Bolivia in Amboro and Noel Kempff Mercado National Parks. In Brazil, common in Amazonia, and present in Tapajós National Park, Pará; in SE Brazil present in Sooretama Biological Reserve, Espírito Santo.

**Bibliography.** Anon. (1998d), Canaday & Jost (1999), Davis, T.J. (1986), Donahue (1994), Echeverri (1986), Iffrench (1991), Friedmann (1948), Friedmann & Smith (1950, 1955), Griscom & Greenway (1941), Guix (1995), Gyldenstolpe (1945b), (1951), Haffer (1975), Haverschmidt & Mees (1994), Herklots (1961), Hilty & Brown (1986), Meyer de Schauensee (1949), Meyer de Schauensee & Phelps (1978), Moonen *et al.* (1941), Oniki & Willis (1983), Oren & Parker (1997), Parker & Goerek (1997), Phelps & Phelps (1958), Pinto (1935, 1938, 1947, 1950), Remsen & Traylor (1989), Ridgely & Gwynne (1989), Rinke *et al.* (1996), Rüschi (1979), Schubert *et al.* (1965), Sick (1985, 1993), Sneathage, E. (1935), Sneathage, H. (1927-1928), Snyder (1966), Stotz *et al.* (1996), Thiollay (1992), Thiollay & Julhen (1998), Tostain *et al.* (1992), Wetmore (1968), Williams & Tobias (1994), Willis & Eisenmann (1979), Zimmer (1948).

17. Baird’s Trogon

*Trogon bairdii*

**French:** Trogon de Baird      **German:** Bairdtrogon      **Spanish:** Trogón de Baird  
**Other common names:** Vermilion-breasted Trogon

**Taxonomy.** *Trogon bairdii* Lawrence, 1868, San Mateo, Costa Rica.

Forms a superspecies with *T. viridis*, *T. citreolus* and *T. melanocephalus*; sometimes considered conspecific with *T. viridis*, differing from race *chionurus* of which mainly in belly colour and female’s undertail pattern, with habits and vocalizations rather similar. Monotypic.

**Distribution.** Pacific slope of Costa Rica (N to around Río Grande de Tárcoles) and adjacent SW Panama (W Chiriquí).



more pointed and with less regular barring; male with little orange on belly, female with none. VOICE. A series of barking notes, first level, then accelerating and falling abruptly, sometimes ter-

**Descriptive notes.** 25-28 cm; 94-95 g. Male has light blue bill and orbital ring; head to mid-breast bluish-black, mid-breast to undertail-coverts deep bright red; upperparts metallic blue-green, wingpanel mostly blackish; primaries whitish on outer webs; tail greenish-blue to violet-blue and tipped black above, almost entirely white below with black tip. Virtually identical to *T. viridis* except for red on underparts. Female duller, greyer, without green and blue tones, dark slate above, paler on throat and breast; red on underparts less extensive; undertail barred, with white bars half width of slaty bars. Juvenile like female, but rectrices

minating with several widely spaced notes on lower pitch; clearer and more melodious than *T. massena*; sharp cackle when agitated.

**Habitat.** Canopy of humid rainforest; sometimes venturing into forest edge, upper understorey, shrubby undergrowth and adjacent tall second growth, or well-shaded semi-open woodland, to visit fruiting trees and shrubs; some use of transitional zone between forest and tropical dry growth. In lowlands and foothills locally to 1200 m.

**Food and Feeding.** Fruit, also insects, including large hairy caterpillars; once a small lizard. Large green insects and larvae brought to young, once a large stick-insect. Sallies to seize fruit and insects from foliage, and takes prey from ground.

**Breeding.** Apr-Aug. Nest a rounded unlined chamber with ascending tunnel, 2-15 m up in large decaying trunk in forest or adjacent clearing. Eggs 2-3; incubation 16-17 days; nestling period c. 25 days.

**Movements.** Apparently sedentary.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Restricted-range species: present in South Central American Pacific Slope EBA. Fairly common in Costa Rica, notably in Terraba Valley, but deforestation in much of range has drastically reduced species’ habitat, restricting it chiefly to a number of protected areas such as Corcovado National Park on the Osa Peninsula, Manuel Antonio National Park and Carara Biological Reserve. Rare in Panama, with most recent record apparently 2 pairs on Burica Peninsula in 1982.

**Bibliography.** Anon. (1998d), Carriker (1910), Collar & Andrew (1988), Engelman (1996a, 1997), Ridgely & Gwynne (1989), Skutch (1962, 1983), Slud (1964), Stattersfield *et al.* (1998), Stiles (1985), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968).

18. Citreoline Trogon

*Trogon citreolus*

**French:** Trogon citrin      **German:** Graukopftrogon      **Spanish:** Trogón Citrino

**Taxonomy.** *Trogon citreolus* Gould, 1835, no locality = Mexico.

Forms a superspecies with *T. viridis*, *T. bairdii* and *T. melanocephalus*; sometimes considered conspecific with *T. melanocephalus*. Two subspecies recognized.

**Subspecies and Distribution.**

*T. c. citreolus* Gould, 1835 - Pacific slope of Mexico from Sinaloa to Oaxaca.

*T. c. sumichrasti* Brodkorb, 1942 - Pacific coastal plain of Mexico in Oaxaca and Chiapas.



**Descriptive notes.** 27 cm. Male nominate race with bill pale blue-grey, eye yellow; head and breast dull greyish-black, creamy white breast-band, yellow rest of underside; wings greyish-black; mantle and back green, rump and uppertail-coverts deep blue; uppertail bluish-green, tipped black; undertail largely whitish with black border. Differs from similar *T. melanocephalus* in greyer, less black, head and breast, yellow eye and no visible orbital ring, less blue tinge to green of back, less black on undertail. Female has rather dark grey head, breast and back, upper mandible partially blackish. Juvenile with dark eye, slightly more

black on undertail. Race *sumichrasti* larger, with broader white tips to outer rectrices. VOICE. Like that of *T. melanocephalus*; rapid series of short notes resembling an antbird (Thamnophilidae).

**Habitat.** Arid to semi-arid open woodland, low coastal jungle and thorny brushland, thorn-forest, scrub, tropical deciduous and lower tropical semi-deciduous forest, second growth, plantations, open humid forest, swamp-forest and mangroves, reaching 1000 m. Chief habitat (“ecological centre”) appears to be thorn-forest.

**Food and Feeding.** Chiefly fruit in Feb-Jun, insects in Jul-Oct, and fruit and insects in equal quantity in Nov-Jan; insects include flying ones and large caterpillars. In one study, fruits included drupes of the small trees *Recchia mexicana* and *Comocladia engleriana*, berries of the vine *Trichostigma octandrum* and syconium of a fig *Ficus pertusa*; fruits of the first 3 were swallowed whole (the larger seeds of first 2 being regurgitated), but those of figs were crushed in bill before swallowing; last 2 were intensively exploited, although the fig was scarce in the area. In another study fruits of *Ehretia tinifolia* important, and in a third *Acacia*, *Byrsinima*, *Casearia*, *Celtis*, *Coccoloba*, *Cupanis*, *Eugenia*, 4 species of *Ficus*, *Paulinia*, *Pithecollobium* and *Vitex* were taken.

**Breeding.** May-Aug. Nest in arboreal termitarium, chiefly of *Nasutitermes*, in relatively sheltered patch of vegetation. Eggs 2-4. No other information.

**Movements.** Apparently sedentary.

**Status and Conservation.** Not globally threatened. Species generally reckoned to be common to fairly common in appropriate habitat throughout most of range, and very common in Oaxaca.

**Bibliography.** Álvarez del Toro (1980), Anon. (1998d), Binford (1989), Blake & Hanson (1942), Eguarte & Martínez del Río (1985), Howell & Webb (1995), Huerta (1994), Hutto (1992), Kantak (1979), Klaas (1968), Lowery & Dalquest (1951), Miller *et al.* (1957), Rowley (1984), Schaldach (1963), Stotz *et al.* (1996).

19. Black-headed Trogon

*Trogon melanocephalus*

**French:** Trogon à tête noire      **German:** Schwarzkopftrogon      **Spanish:** Trogón Cabecinegro

**Taxonomy.** *Trogon melanocephala* Gould, 1835, Tamalulipas, Mexico.

Forms a superspecies with *T. viridis*, *T. bairdii* and *T. citreolus*; sometimes considered conspecific with *T. citreolus*. Populations of W Costa Rica described as race *illaetabilis* on basis of paler belly, but this character apparently not constant. Original description clearly treats species name as adjective: hence this becomes masculine to agree with genus name. Monotypic.

**Distribution.** Atlantic slope of SE Mexico (including islands off Quintana Roo), N Guatemala, Belize, and N Honduras; also Pacific slope of El Salvador, and Nicaragua and N Costa Rica.

**Descriptive notes.** 27 cm; 69-91 g. Male with bill pale blue-grey, orbital ring pale blue; head and breast dull blackish; white breastband, yellow rest of underside; wings greyish-black, primaries whitish on outer web; mantle and back bluish-green, rump and uppertail-coverts deep blue; uppertail bluish-green, tipped black; undertail blackish, with broad square white tips forming block of dark-bordered white. Female like male, but blackish and bluish-green replaced with greyish-black, dark-



est on face and throat, and has narrower white tips on undertail; upper mandible partly blackish. Juvenile mostly greyish-brown, wing-coverts spotted buff, belly to vent whitish with dusky blotching; immature like respective adult but duller, secondaries spotted white, outer webs of white undertail barred basally. **Voice.** Song a series of quickening clear barks, falling in pitch and stopping rather abruptly, "ñah-ñah-ñah-ñahñahñah", harsher, more nasal, less resonant than *T. bairdii*. Also hollow thrush-like clucks and various rolled calls.

**Habitat.** Species of natural open and secondary formations. Usually fairly low in open deciduous woodland and evergreen gallery forest, forest edge, fringes of riverine wooded belts through

cleared areas, tall or light second-growth woodland, bushy scrub and thickets, semi-open areas with scrub and trees, mangroves, partially cleared lands and lowland pastures with scattered trees, and edges of plantations, in both humid and semi-arid regions, the latter mostly on Pacific slope; sea-level to 1000 m, but chiefly below 600 m. In Yucatán in all wooded habitats except dense rainforest and coastal scrub. In El Salvador commonest at coast, preferring swampiest, most humid localities, including mangroves. In Belize most frequent in medium to tall second growth and forest border, but also in pinelands and among scattered trees. In Honduras prefers humid lowland second growth or open woodland to dense forest, and is fairly common in monsoon forest and arid scrub on Pacific slope. In Costa Rica in scrubby cattle country, bushy and shrubby portions of farmland, thinned or second-growth woodland with bushy and thickety clearings.

**Food and Feeding.** Insects and fruits. Animal food includes Orthoptera (grasshoppers), mantises, dragonflies, large caterpillars (smooth and hairy, including Spingidae). Vegetable food includes arillate seeds such as *Trichilia*, green fruiting spikes of *Cecropia*, berries, drupes such as *Spondias*, oranges opened by woodpeckers, pulp of the rubber tree *Castilla*, and various berries. Salies from perch to seize insect or snatch fruit.

**Breeding.** May-Jun in Belize, Mar-Jul in Costa Rica. Nest an unlined chamber in an occupied terrarium 1.5-8 m up in tree, on fence post or on other low support. Eggs 3; incubation 19 days; nestling period 16-17 days.

**Movements.** Resident in Mexico. In Costa Rica, strays S to head of Golfo Dulce and E to Grecia along river bottoms in W Valle Central.

**Status and Conservation.** Not globally threatened. Common to fairly common in Mexico; found throughout Yucatán, where the commonest trogon. Most numerous trogon also throughout Belize; found to be common in Guatemala in 1960's; common in El Salvador, and commonest trogon of semi-open situations in lowlands of both coasts in Honduras; abundant in Nicaragua; common in Costa Rica.

**Bibliography.** Anon. (1988d), Binford (1989), Brodtkorb (1943), Carraker (1910), Dearborn (1907), Dickey & van Rossem (1938), González-García (1993), Howell & Webb (1995), Land (1970), Monroe (1968), Paynter (1955), Russell (1964), Salvin & Godman (1888-1904), Skutch (1948, 1983), Slud (1964, 1980), Smithe (1966), Stiles & Skutch (1989), Stotz *et al.* (1996), Vallely & Whitman (1997), Van Tyne (1935), Wetmore (1943).

## 20. Violaceous Trogon

### *Trogon violaceus*

**French:** Trogon violacé      **German:** Veilchentrogan      **Spanish:** Trogón Violáceo  
**Other common names:** Gartered Trogon (*caligatus*), Amazonian Trogon (*ramonianus*)

**Taxonomy.** *Trogon violaceus* J. F. Gmelin, 1788, no locality = Surinam.

Sometimes placed in separate genus *Chrysotrogon*. DNA studies suggest possibly closest to *T. viridis* and *T. eurucui*. Races *caligatus* and *ramonianus* have both been treated as separate species by some authors. Northernmost race commonly labelled as *braccatus*, but name *sallaei* has priority. Extensive individual variation in degree of bronzy tinge on back in nominate and race *caligatus* led to description of *rossi*, now considered a synonym of nominate. Six subspecies recognized.

#### **Subspecies and Distribution.**

*T. v. sallaei* Bonaparte, 1856 - Caribbean slope of E & S Mexico, also Pacific slope of S Mexico, and Guatemala, Belize, El Salvador and N Honduras; possibly this race in Nicaragua.

*T. v. concinnus* Lawrence, 1862 - Costa Rica, Panama (except Caribbean slope of Darién), W Colombia, W Ecuador and NW Peru.

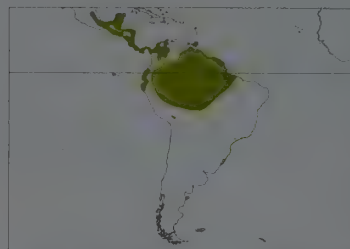
*T. v. caligatus* Gould, 1838 - NE Panama (Caribbean slope of Darién) into N Colombia and W Venezuela.

*T. v. violaceus* J. F. Gmelin, 1788 - E Venezuela, the Guianas and adjacent N Brazil; Trinidad.

*T. v. ramonianus* Deville & Des Murs, 1849 - Amazonian areas of Colombia, Ecuador, Peru, Bolivia and Brazil; also penetrates S Venezuela (upper R Orinoco).

*T. v. crissalis* (Cabanis & Heine, 1863) - NE Brazil on S bank of lower R Amazon and tributaries (E of R Tapajós).

**Descriptive notes.** 23-25 cm; 38-57 g. Male nominate race has bill pale blue-grey, orbital ring pale yellow; head to mid-breast violet-blue, with mask and throat black, white breastband shading into bright yellow on rest of underside; upperparts metallic green, wingpanel indistinctly vermiculated black and white (appearing dark grey-brown at distance); flight-feathers dark, primaries whitish on outer webs; tail relatively short, violet-blue and tipped black above, finely barred black and white below with broader white tips forming 3 bands. Differs from very similar *T. rufus* chiefly in colours of head and voice. Female has blackish culmen, white eyering broken above and below eye, lacks



violet-blue and green, has wingpanel densely barred black and white, belly duller yellow with grey wash on flanks, undertail with black inner webs creating pied and barred effect. Immature male like adult but with browner wingpanel, undertail with less white; juvenile like female. Race *sallaei* has blackish head and breast, blue nape and lower edge of breast, more golden upperparts, wingpanel densely barred grey and white (appearing pale grey), greener uppertail; *concinnus* similar but with bluer upperparts and uppertail; *caligatus* has head like nominate, upperparts and tail like *concinnus*, wingpanel well marked (appearing

mid-grey); *ramonianus* male differs from nominate in having even fainter or no vermiculations on wingpanel, stronger blue crown, breast and central tail feathers, culmen sharply ridged; *crissalis* has head black, glossed purple-blue on hindcrown. **Voice.** Song is a long series of rapid hollow downslurred whistles, "kyu-kyu-kyu-kyu-kyu", without acceleration of *T. viridis* and higher-pitched than *T. massena*, recalling Ferruginous Pygmy-owl (*Glaucidium brasilianum*); calls include rolling chattering.

**Habitat.** In N of range appears to enter primary evergreen forest, heavy and light rainforest (common in such habitat in Oaxaca, Mexico, less so in semi-deciduous and Pacific swamp-forest), but also tall second growth (especially near streams), clearings, open woodland and second growth, edge, plantations and mangroves, occupying middle to upper storeys; where broadly sympatric with *T. rufus*, generally prefers more open forest and second growth, forest borders, thinned woodland and, especially, shaded plantations (cacao, coffee) and openings with shrubs and trees; although 1800 m or 1850 m cited as elevation limit in Central America, recorded with certainty only to 1400 m. In Costa Rica occupies canopy in drier areas (e.g. evergreen gallery forest), but in wetter areas found in forest edge, semi-open parts, clearings with scattered tall trees and tall second growth, to 830 m on Caribbean slope, to 1200 m on Pacific slope. Not a forest-interior bird in Panama and Colombia, occurring at borders, and in shady and lighter second-growth woodland, and clearings with scattered trees, to at least 1000 m; to 1200 m in Venezuela. In Surinam found in sand-ridge forest, savanna areas and interior forest. In Amazonia prefers canopy and edges of transition forest, *terra firme* forest and *igapó* (permanently flooded forest).

**Food and Feeding.** Fruit and small invertebrates. Possibly more frugivorous than other trogons, since several stomachs of birds from El Salvador held just fruit pulp, and 4 contained exclusively mistletoe berries; also recorded taking *Cecropia* fruit, *Didymopanax morototoni* berries, and oranges opened by Golden-fronted Woodpecker (*Melanerpes aurifrons*). Invertebrate food includes caterpillars, ants, wasps, termites, katydids, locusts, earwigs and spiders. Nestlings fed on insects and small fruits. Salies, hovering to pluck fruits and insects from vegetation; often feeds in low trees on berries and fruit alongside thrushes (Turdidae) and tanagers (Thraupidae). When taking over a wasp nest, the birds catch and apparently eat the wasps, sustaining the assault for up to 2 weeks. Joins mixed-species flocks.

**Breeding.** Mar-Jun in Mexico; inferred May/Jun in Belize; May-Jul in El Salvador; Feb-Jun in Costa Rica; birds in breeding condition in Mar in Colombia; young in Jan in Panama; Feb in Venezuela; Nov, Feb, Mar, May and Jun in Trinidad. Nest in very large, turbinate arboreal vespiary (e.g. of *Parachatergus*, composed of silvery-grey paper), mainly 10-15 m up at edge of or outside forest, or in arboreal nest of *Azteca* ants, or in termitary, rotten trunk, or root-mass of ferns (once possibly *Polypodium crassifolium*) or other epiphytes. Eggs 2-3; nestling period at least 17 days. No further information.

**Movements.** Resident in Mexico; probably also elsewhere, but no definite information available. **Status and Conservation.** Not globally threatened. Common to fairly common in Mexico, where abundant in upper tropical zone of Veracruz in 1940's, but not abundant in Yucatán. Common in lower tropical zone of El Salvador in 1930's. Commonest and most widespread trogon in lowland Guatemala; fairly common in the Pacific and Caribbean subtropics and lowlands, less numerous in Petén, but seemingly increasing at Tikal with opening-up of woodland. Moderately common in Belize and Honduras. Uncommon and local in dry NW Costa Rica; common in more humid areas, and once considered the most abundant and widespread member of family there, but always commonest in lowlands. Fairly common in Panama. Recently recorded for first time on Pacific slope of SW Colombia, whither may have spread from W Ecuador, as a result of continuing deforestation of SW Colombia. In Venezuela, race *caligatus* formerly widespread in Sierra de Perijá, whence no recent information, local elsewhere; *ramonianus* and *violaceus* both local. Common in Trinidad, also in Surinam. Common in Amazonian Brazil, and present in Tapajós National Park, Pará. Generally uncommon but unobtrusive in Peru, where rare in arid tropical zone and frequent in humid tropical zone; in floodplain-forest, territory c.14 ha and 3-5 pairs/km<sup>2</sup>. Present in Bolivia in Beni Biological Station and Amboró and Noel Kempff Mercado National Parks. Increases noted in logged forest.

**Bibliography.** Álvarez del Toro (1980), Anon. (1998d), Binford (1989), Browning *et al.* (1991), Carraker (1910), Cohn-Haft *et al.* (1997), Dickey & van Rossem (1938), Donahue (1994), ffrench (1991), Friedmann (1948), González-García (1993), Griscom (1932), Griscom & Greenway (1941), Gyldenstolpe (1951), Haffer (1975), Haverschmidt & Mees (1994), Hilty & Brown (1986), Howell & Webb (1995), Land (1970), Lowery & Dalquest (1951), Meyer de Schauensee (1949), Meyer de Schauensee & Phelps (1978), Monroe (1968), Oren & Parker (1997), Paynter (1955), Peres & Whittaker (1991), Phelps & Phelps (1958), Pinto (1938, 1947, 1950), Remsen & Traylor (1989), Ridgely & Gwynne (1989), Ruschi (1979), Russell (1964), Schubart *et al.* (1965), Sick (1985, 1993), Skutch (1972a, 1981, 1994, 1999), Slud (1960, 1964), Smithe (1966), Stiles & Skutch (1989), Stotz *et al.* (1996), Strewé (2000), Terborgh *et al.* (1990), Thiollay (1992), Tostain *et al.* (1992), Walters (1986), Wetmore (1968), Wiedenfeld *et al.* (1985), Zimmer (1948).









## 21. Mountain Trogon

### *Trogon mexicanus*

**French:** Trogon montagnard      **German:** Bronzetrogon      **Spanish:** Trogón Mexicano  
**Other common names:** Mexican Trogon

**Taxonomy.** *Trogon Mexicanus* Swainson, 1827, Temascaltepec, Mexico. Possibly most closely related to *T. elegans*, *T. collaris*, *T. personatus*, *T. rufus* and *T. curucui*. Birds from Honduras sometimes separated as race *lutescens*, but apparently indistinguishable from nominate. Two subspecies recognized.

#### **Subspecies and Distribution.**

*T. m. clarus* Griscom, 1932 - NW Mexico.

*T. m. mexicanus* Swainson, 1827 - W, E & S Mexico, S Guatemala, S Honduras and N El Salvador.



pale brown lower breast, red belly to undertail-coverts; uppertail rufous, tipped black, undertail with barred outer webs, mostly black inner webs and white tips. Young birds resemble female, but with buffy spots on coverts, ring of bare yellow skin around eye, buff belly. Race *clarus* female paler from ear-coverts to breast. **Voice.** Song a series of 3-15 double whistles, "kyow-kyow kyow-kyow kyow-kyow", sometimes followed by softer accelerating run of 10-14 notes, "hu-hu-hu-hu-hu-hu-huhuhuhu"; calls include clucks and cackling chatters.

**Habitat.** Inhabits middle to upper storeys of pine-oak and pine-evergreen ("cypress") and humid montane forest in Mexican highlands, at 1200-3500 m, rarely lower. In Guatemala, shows marked preference for the oak-and-cypress belt within W mountains, at 800-2900 m. Pine and pine-oak forest above 1200 m (sometimes down to 600 m) in Honduras. Tolerates second growth.

**Food and Feeding.** Food brought to young included green and white larvae, moths, mantises. May associate loosely with mixed-species flocks.

**Breeding.** Apr-Jun in Mexico, Mar-May in Guatemala. Nest in tree cavity or rotten stump, generally very low down, sometimes 0-5 m from ground. Eggs 2-3; incubation 19 days; nestling period 15-16 days.

**Movements.** Largely resident; occasionally moves into lower pine-oak habitat in colder dry-season months, returning upslope at start of wet season to breed; in Chiapas considered probably partial altitudinal migrant. Apparently partial migrant in N of range; has occurred within 160 km of USA border.

**Status and Conservation.** Not globally threatened. Common to fairly common in Mexico; found in low numbers in El Triunfo Biosphere Reserve, and in Oaxaca common (sometimes abundant) in humid pine-oak forest and uncommon in arid pine-oak forest. The common trogon of mountains of W Guatemala; locally common in Sierra de las Minas. Uncommon to fairly common in interior Honduras.

**Bibliography.** Álvarez del Toro (1980), Anon. (1998d), Binford (1989), Blake & Hanson (1942), Dearborn (1907), Eckelberry (1963), Gómez de Silva *et al.* (1999), Griscom (1932), Howell & Webb (1995), Jones (1998), Land (1970), Miller *et al.* (1957), Monroe (1968), Parker *et al.* (1976), Rowley (1966), Salvin & Godman (1888-1904), Schaldach (1963), Skutch (1942, 1983), Stotz *et al.* (1996), Thurber *et al.* (1987), Wetmore (1941), Wilson & Ceballos-Lascuráin (1993).

## 22. Elegant Trogon

### *Trogon elegans*

**French:** Trogon élégant      **German:** Kupfertrogon      **Spanish:** Trogón Elegante  
**Other common names:** Coppery-tailed Trogon ("ambiguous group")

**Taxonomy.** *Trogon elegans* Gould, 1834, Guatemala.

Possibly most closely related to *T. mexicanus*, *T. collaris*, *T. personatus*, *T. rufus* and *T. curucui*. DNA studies suggest that middle three of these may be closest to present species. Races generally regarded as falling into two groups, "ambiguous group" N of Isthmus of Tehuantepec and "elegant group" S of there, these sometimes regarded as representing two separate species. Birds in El Salvador and Honduras intermediate between *elegans* and *lubricus*. Populations in S Arizona and NW Mexico (excluding Tres Marias Is) sometimes separated as race *canescens*. Four subspecies recognized.

#### **Subspecies and Distribution.**

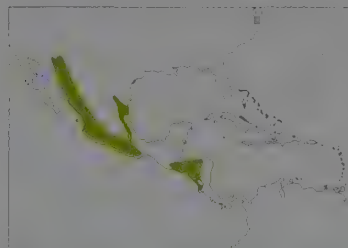
*T. e. goldmani* Nelson 1898 - S Arizona, and NW Mexico (including Tres Marias Is).

*T. e. ambiguus* Gould, 1835 - E & SC Mexico.

*T. e. elegans* Gould, 1834 - Guatemala (Motagua Valley), extending into El Salvador and Honduras.

*T. e. lubricus* J. L. Peters, 1945 - Nicaragua and NW Costa Rica.

**Descriptive notes.** 28-30 cm; 67 g. Male nominate race with bill yellow, orbital ring orange-red; face and throat blackish; crown to upperparts and lower throat to mid-breast green; white breastband, with red below; greyish wingpanel; primaries with whitish outer webs; uppertail bronzy with black tip, undertail barred black and white with broad white tips. Differs from *T. mexicanus* in uppertail colour, undertail pattern, whitish outer webs of primaries. Female grey-brown, with white breastband, paler brown lower breast, red lower belly to vent, white vertical bar on ear-coverts; differs from female *T. mexicanus* in greyer coloration, white on ear-coverts, broader dark tail tip. Immature like respective adult but duller, with slimmer, more coarsely barred rectrices, male with white centre of belly, faint ear-covert bar; juvenile mostly dull brown, belly to vent mottled and barred brown and white, wing-coverts spotted white. Race *lubricus* with more numerous and broader black bars on wingpanel, female warmer brown; *ambiguous* and



*goldmani* have undertail white with vague barring, *goldmani* also with bronze and coppery gloss above, paler red below, and female paler brown. **Voice.** Song a series of 3-11 rapidly repeated, hoarse, downslurred "kwa'h" or "coa" notes; calls include rolled chattering and churring notes.

**Habitat.** Usually found in canopy of arid or semi-arid open woodland, pine-oak forest, deciduous riparian woods in pine zones, scrubby woodland and second growth, thorn-forest, gallery formations; less frequently in humid evergreen forest, at least in N of range. From lowlands to 2400 m in Mexico (vertical range

apparently wider in S than in N), and to 1800 m in Central America, although only to 750 m in Costa Rica; often on hillsides and in ravines and gulleys. Uses dense brush under 4 m high, and secondary scrub, but usually in taller, denser dry forest than *T. melanocephalus*. In S Arizona, common overstorey trees in canyons where nesting occurred were *Juniperus deppeana*, *Pinus cembroides*, *P. engelmannii*, *P. leiophylla*, *Quercus hypoleucoides*, *Q. emoryi*, *Q. reticulatum* and *Q. arizonica*, with the sycamore *Platanus wrightii* and various other trees along watercourses. 1500-2500 m; the sycamores were favoured for nesting (80% of 46 sites). Habitat in Oaxaca poorly understood, but includes humid and arid pine-oak forest and short-tree tropical deciduous forest, at 700-2100 m. In Guatemala, occurs in scrubby woodland and plantations, from near sea-level up to 1900 m. In Honduras, typically in arid portions and interior Caribbean valleys, entering monsoon forest.

**Food and Feeding.** Chiefly fruit in Feb-Jun, insects in Jul-Oct, and fruit and insects in equal quantities in Nov-Jan. Fruit includes *Acacia*, *Byrsonima*, *Casearia*, *Celtis*, *Coccoloba*, *Cupanis*, *Eugenia*, 4 species of *Ficus*, *Paullinia*, *Pithecollobium* and *Vitex*; also takes berries and arillate seeds. Insect food includes grasshoppers, mantises, bugs, beetles, moths and caterpillars; also eggs and larvae. Insects fed to young include Orthoptera, Lepidoptera, Coleoptera, Homoptera, Hymenoptera, Odonata and Mantoidea; also berries just before fledging. Sallies to seize insects and fruit from among foliage; once also seen taking flower of *Hura polyandra*.

**Breeding.** May-Aug in USA and El Salvador, Mar-Jul (often 2 broods) in Mexico. Nest an unlined (perhaps sometimes lined) cavity in low rotting trunk 2-6 m up in tree, usually in relatively open area; reportedly also, rarely, in earth bank; in S Arizona, 83% of 59 nests were old woodpecker holes. Eggs 2-3; incubation 19 days; nestling period 15-16 days.

**Movements.** Apparently mostly resident; N populations partially migratory, moving into Arizona from N Mexico in mid-Apr; casual visitor (*ambiguus*) to S Texas, in lower Rio Grande Valley and at Big Bend. Makes daily movements from riparian woodland up dry gulleys and into pines on slopes.

**Status and Conservation.** Not globally threatened. Common to fairly common in much of range; in N thought to fluctuate in numbers between years. In Mexico, uncommon in Oaxaca and rare in El Triunfo Biosphere Reserve; in Guatemala, fairly common in upper Motagua Valley and in drier parts of Pacific lowlands and subtropics; in Honduras, generally uncommon or absent, but fairly common in monsoon forest; uncommon to locally common in N Pacific lowlands in Costa Rica. Species is, however, particularly susceptible to disturbance in breeding season, e.g. in Arizona, where disturbance thought responsible for near-total breeding failure of population.

**Bibliography.** Allen (1944), Anon. (1998d), Arnold (1984), Baicich & Harrison (1997), Bent (1940), Binford (1989), Brown (1973), Corcuera & Butterfield (1999), Cully (1986), DeGraaf & Rappole (1995), Devine *et al.* (1978), Dickey & van Rossem (1938), Elliott (1983), Griscom (1932), Hakes (1983), Hall (1996a), Hall & Karubian (1996), Howell & Webb (1995), Huerta (1994), Kaufman (1996), Kunzmann *et al.* (1998), Land (1970), Marshall (1957), Monroe (1968), Noeddal (1988), Parke (1993), Parker *et al.* (1976), Pearson (1936), Price *et al.* (1995), Rappole & Blacklock (1994), Ridgway (1887a, 1887b), Salvin & Godman (1888-1904), Schaldach (1963), Slud (1964), Stiles & Skutch (1989), Stotz *et al.* (1996), Taylor, R. (1978b, 1978c, 1979, 1980a, 1980b, 1980c, 1981, 1982, 1994), Walters (1997), Webster (1984).

## 23. Collared Trogon

### *Trogon collaris*

**French:** Trogon rosalba      **German:** Jungferntrogon      **Spanish:** Trogón Acolarado  
**Other common names:** Bar-tailed(!)/Jalapa Trogon (*puella*); Orange-bellied Trogon ("aurantiiventris")

**Taxonomy.** *Trogon collaris* Vieillot, 1817, Cayenne.

Possibly closest to *T. mexicanus*, *T. elegans*, *T. personatus*, *T. rufus* and *T. curucui*; DNA studies suggest that nearest relatives may be middle three of these. Orange-bellied birds from Costa Rica and W Panama, described as *aurantiiventris*, sometimes treated as a separate species, and assortative pairing has been reported; since an identical individual has been taken in S Mexico (Oaxaca), however, this form is now considered to be no more than a morph of present species. Race *puella* sometimes regarded as a distinct species. Validity of race *extimus* questionable. Proposed race *xalapensis* (Jalapa) considered indistinguishable from *puella*; *eytoui* (Rio de Janeiro) apparently inseparable from *castaneus*; considerable uncertainty also attends status of proposed races *underwoodi* from NW Costa Rica and *flavidiator* from Panama (Cerro Flores). Eight subspecies recognized.

#### **Subspecies and Distribution.**

*T. c. puella* Gould, 1845 - E Mexico S along both slopes of Central America to C Panama (Veraguas).

*T. c. extimus* Griscom, 1929 - NE Panama (E Darién).

*T. c. heothinus* Wetmore, 1967 - E end of Serranía del Darién.

*T. c. virginialis* Cabanis & Heine, 1863 - W Colombia and W Ecuador.

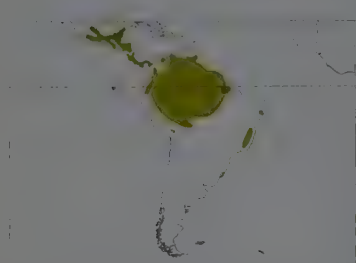
*T. c. subtropicalis* Zimmer, 1948 - subtropical zone of W Colombia in Magdalena and Cauca Valleys.

*T. c. exoptatus* Cabanis & Heine, 1863 - N Venezuela.

*T. c. collaris* Vieillot, 1817 - E of Andes (except N Venezuela) S to N Bolivia and WC Brazil; Trinidad and Tobago.

*T. c. castaneus* Spix, 1824 - lower Amazon and patchily in E Brazil.

**Descriptive notes.** 25-29 cm; 41-70 g. Male nominate race with bill yellow, orbital ring orange-red; face and throat blackish; crown, nape, upperparts, and lower throat to mid-breast green or bluish-green; white breastband, with red below; wingpanel barred black and white; outer webs of primaries white; uppertail blue-green with black tip, undertail black with narrow white barring. Differs from *T. mexicanus* in more distinctly barred wingpanel, white in primaries, undertail pattern. Female



with dark upper mandible, white broken eyering, brown crown, upperparts and breast, pale red lower breast to undertail-coverts, deep rufous uppertail, undertail whitish mottled dusky with single narrow subterminal bar on each feather; differs from female *T. mexicanus* in more extensive red below, deeper rufous uppertail, pattern of undertail. Immature male has wingpanel brownish, equal black and white bars on undertail, immature female has more dusky mottling on undertail; juvenile mostly rich brown, mixed with buff on breast, shading to deep buff on belly, vent rufous, wing-coverts spotted with buff. Race *puella* has

narrow barring on undertail, with much smaller white tips, in morph "*aurantiventris*" red below replaced with orange (sometimes darkening towards red); *extimus* small; *heothinus* like *puella*, but white bars on tail broader, no orbital ring; *virginalis* with back richer green, tail with broad terminal white tips (not so broad as nominate) and narrower bars, female slightly paler than nominate or *puella*; *subtropicalis* longer-winged than neighbouring forms, wingpanel more finely barred, green of head and breast less bluish than *virginalis*; *exoptatus* with upperparts, breast and central tail feathers shining coppery-green, longer tail, female with dusky mottled undertail; *castaneus* with wingpanel more coarsely marked than nominate. Voice. Song 2-4 clear mellow descending notes, "kyow-kyow" or "kyow-kyow-kyow", sometimes delivered faster and becoming accelerated laugh, very similar to *T. rufus*, but variable, in South America locally more notes, up to 9. Calls include rolling growl, sometimes steadily repeated.

**Habitat.** Primarily an edge species, occupying mostly middle levels of wet, humid and semi-humid tropical evergreen and semi-deciduous forest, open woodland, plantations, cloudforest, pine-evergreen forest, from lowlands (but mostly above 700 m) to 2400 m, in South America possibly to 3100 m. In Yucatán found in tall second growth in both high deciduous forest and, rarely, light rainforest, but in Central America more frequent in foothills and mountains; on Pacific slope from Guatemala to NW Costa Rica only in highland regions, centre of distribution in Costa Rica following upper half of subtropical belt and lower half of lower montane belt, where hilly terrain causes discontinuities in forest height and density, so that edge habitats abundant. E of Andes almost in *virzeza*, but, although occupying coastal woodland in French Guiana, in Surinam it seems to prefer the slightly higher levels of interior forest. In Peru, found in understorey and subcanopy of transition and *terra firme* forest, sometimes in *Guadua* bamboo thickets. Sometimes occurs alongside *T. viridis* and *T. curucui*.

**Food and Feeding.** Somewhat more insectivorous than most Neotropical trogons, taking beetles, Homoptera, caterpillars (including hairy types), Orthoptera and stick-insects. Also many small fruits, including (taken by morph "*aurantiventris*") *Hasseltia floribunda* (in particular), *Rubus*, and species of Ericaceae, Myrtaceae, Rubiaceae, Lauraceae and Symplocaceae. Often follows mixed-species flocks.

**Breeding.** Mar-Jun in Mexico (elevation tending to cause fresh laying in May/June); Apr in Belize; Jan-Apr in Costa Rica (morph "*aurantiventris*" Mar-May, once Jul); birds in breeding condition (and other evidence) Jan-May in Colombia; Apr-Jun in Venezuela, Mar and May in Trinidad, and Nov-Dec in French Guiana. Nest a shallow unlined niche or a more enclosed cavity 1.2-5 m up in decaying stub, rotten stump or snag, often in clearing; use of arboreal termitaria reported in French Guiana and Trinidad. Eggs 2-3; nestling period c. 16 days.

**Movements.** Largely resident. In Mexico, thought possibly a partial altitudinal migrant in Chiapas; 3 records from Atlantic lowlands in Oaxaca probably represent rare winter displacements. In Costa Rica, sometimes wanders up to at least 2800 m and, following breeding, down to 150 m on Caribbean slope and to 600 m on Pacific.

**Status and Conservation.** Not globally threatened. Common to fairly common in Central America. In Mexico, found in small numbers in El Triunfo Biosphere Reserve, Chiapas, and rarest trogon in Yucatán; in Guatemala commonest in lower subtropical zone, ranging down into foothills, but rare in Petén; rare in Belize; in Honduras uncommon within altitudinal range, except at 600-1000 m. Common in Costa Rica, with morph "*aurantiventris*" uncommon to fairly common in Cordilleras de Tilarán and de Guanacaste, but rare and local on Cordilleras Central and de Talamanca alongside red-bellied *collaris*. Fairly common in Panama, where "*aurantiventris*" uncommon to fairly common in Chiriquí and W Panamá Province, most numerous on Cerro Campana (from which red-bellied *collaris* absent). In Colombia fairly common to common, generally less so E of Andes than W; fairly common in Los Nevados National Park, uncommon in Munchique National Park. Present in Podocarpus National Park in Ecuador. Variable abundance in forest in Peru; in floodplain-forest territory c. 8 ha and as many as 8 pairs/km<sup>2</sup>, but uncommon to fairly common at 750-1450 m in N Peru, and uncommon in Tambopata. Present in Bolivia in Beni Biological Station and Amorbó and Noel Kempf Mercado National Parks. In Brazil, present in numerous protected areas, e.g. Tapajós National Park, Pará, and Sooretama Biological Reserve, Espírito Santo. In Surinam somewhat local, and only fairly common to common at moderately elevated sites (450-700 m) such as Nassau tablelands, Brownsberg, Lely Gebergte. Fairly common in N Trinidad, but in early 1990's still recovering on Tobago from effects of 1963 hurricane.

**Bibliography.** Álvarez del Toro (1980), Anon. (1998d), Binford (1989), Bond *et al.* (1989), Davis, T.J. (1986), Dickey & van Rossem (1938), Donahue (1994), Iffrench (1991), González-García (1993), Griscom (1932), Gyldestolpe (1951), Haverschmidt & Mees (1994), Herklots (1961), Hilty & Brown (1986), Howell & Webb (1995), Land (1970), Lowery & Dalquest (1951), Meyer de Schauensee (1949), Meyer de Schauensee & Phelps (1978), Miller (1963), Monroe (1968), Oren & Parker (1997), Paynter (1955), Phelps & Phelps (1958), Pinto (1935, 1950), Pople *et al.* (1997), Rasmussen *et al.* (1994), Remsen & Traylor (1989), Ridgely & Gwynne (1989), Rowley (1966, 1984), Ruschi (1958), Russell (1964), Rutgers & Norris (1977), Salvin & Godman (1888-1904), Sick (1985, 1993), Skutch (1956, 1983), Slud (1960, 1964), Smith (1966), Stiles & Skutch (1989), Stotz *et al.* (1996), Teixeira *et al.* (1986), Terborgh *et al.* (1990), Thiollay & Jullien (1998), Thurber *et al.* (1987), Todd (1943), Tostain *et al.* (1992), Wetmore (1968), Wheelwright *et al.* (1984), Williams & Tobias (1994), Zimmer (1930, 1948).

## 24. Masked Trogon

### *Trogon personatus*

**French:** Trogon masqué **German:** Maskentrogon **Spanish:** Trogón Enmascarado  
**Other common names:** Highland Trogon (*temperatus*)

**Taxonomy.** *Trogon personatus* Gould, 1842, Choachí (1996 m), Colombia. Possibly closest to *T. mexicanus*, *T. elegans*, *T. collaris*, *T. rufus* and *T. curucui*; DNA studies suggest that middle three of these may be nearest relatives. Nine subspecies recognized.

#### Subspecies and Distribution.

*T. p. sanctaemariae* Zimmer, 1948 - N Colombia (Santa Marta massif).

*T. p. personatus* Gould, 1842 - subtropical montane zones of N Colombia and W Venezuela, and C & E Andes of Colombia S to E Peru.

*T. p. assimilis* Gould, 1846 - W Andes of Colombia, W Ecuador and NW Peru.

*T. p. temperatus* (Chapman, 1923) - humid temperate zone of C & E Andes of Colombia and Ecuador.

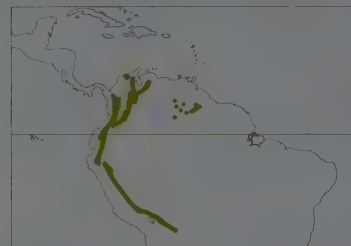
*T. p. duidae* Chapman, 1929 - SC Venezuela (Amazonas and NW Bolívar).

*T. p. paritipui* Zimmer & Phelps, Sr., 1946 - SE Bolívar on Paritipui and others.

*T. p. roraimae* (Chapman, 1929) - SE Bolívar on various cerros, and Roraima part of Guyana.

*T. p. heliothrix* Tschudi, 1844 - temperate zone of Peru.

*T. p. submontanus* Todd, 1943 - Andes of SE Peru (Puno) and Bolivia (including Chuquisaca).



**Descriptive notes.** 25 cm; 64 g. Male nominate race with bill yellow, orbital ring orange-red; face and throat blackish; crown to upperparts and lower throat to mid-breast blue-green; red below white breastband; wingpanel very finely barred black and white (grainy appearance); outer webs of primaries white; uppertail coppery- or brassy-green with black tip, undertail black with very narrow, almost invisible, white barring and broad white tips. Extremely similar to *T. collaris*, but with more bluish tinge to green feathering, much finer barring on wingpanel and undertail, coppery cast to green of uppertail. Female with white

broken eyering, brown crown, upperparts and breast, pale red lower breast to undertail-coverts, uppertail rufous with black tip; differs from female *T. collaris* in all-yellow bill, black face and throat, finely barred undertail. Juvenile presumably similar to that of *T. collaris*. Race *santaemariae* with stronger pale markings on wingpanel; *roraimae* like nominate but smaller, central tail feathers deep coppery-bronze, crown, back and breast brassier, broader white bars on tail; *duidae* like *roraimae*, but outer 3 tail feathers more narrowly marked with white; *paritipui* like *roraimae*, but female with pectoral band more olivaceous; *temperatus* with small bill, bars on outer tail feathers narrow and indistinct, crown and breast bluer, female with white (not brown) lines on wingpanel; *assimilis* midway between nominate and *temperatus* in bill size, uppertail colour and undertail pattern, with finer wingpanel markings than either; *heliothrix* with rather small bill, slightly more bluish-green central tail than *personatus* or *assimilis*, outer 3 rectrices more strongly barred than in *assimilis* or *temperatus* but less than in *personatus*; *submontanus* like *temperatus* but larger-billed, male generally paler, female duller. Voice. Song a soft steady series of 4-8 "kwa" notes, pitch somewhat higher than *T. collaris*; also a descending trill, often repeated.

**Habitat.** Subcanopy and sapling undergrowth of humid and wet forest, mossy forest and cloudforest, forest edge, and second growth and open woodland in broken mountainous country. In Colombia, at 700-2100 m in Santa Marta massif, 1400-2900 m (once as low as 180 m) in Sierra de Perijá, 1000-2500 m (once 3300 m) in W Andes, 2300-3500 m in C of Andes and 1900-3600 m in E Andes; in Ecuador at 1400-2950 m; in Venezuela 1500-3000 m N of R Orinoco, 700-1850 m S of it.

**Food and Feeding.** Fruits of various Clusiaceae and Piperaceae, and insects, all taken in flight. Recorded following mixed-species flocks in Ecuador.

**Breeding.** Birds in breeding condition in Apr-Aug in Colombia. Nest in hole carved into half-rotten wood, in one case 3 m from ground. Eggs 2. No other information available.

**Movements.** None reported, but some vertical displacements seem likely to occur.

**Status and Conservation.** Not globally threatened. Fairly common. In Colombia recorded in Cueva de los Guácharos, Munchique, Los Nevados and Las Orquídeas National Parks, and common in last 2 although hunted in Las Orquídeas by local farmers for its feathers as house ornaments. In Ecuador found in Podocarpus National Park; widespread in Andes and tepuis of Venezuela; frequent in humid temperate and subtropical zones in Peru, but uncommon lower in humid upper tropical zone; present in Bolivia in Amorbó National Park and recently found to be common in the Vallegrande area of Chuquisaca.

**Bibliography.** Allen (1998), Barrowclough *et al.* (1995), Bloch *et al.* (1991), Butler (1979), Chapman (1931), Echeverri (1986), Fjeldså & Krabbe (1990), Fjeldså & Mayer (1996), Gilliard (1941), Hilty & Brown (1986), Mayr & Phelps (1967), Meyer de Schauensee (1947, 1949, 1982), Meyer de Schauensee & Phelps (1978), Miller (1963), Phelps & Phelps (1958), Rasmussen *et al.* (1994), Remsen & Traylor (1989), Ridgely & Gaulin (1980), Ruschi (1979), Sick (1985, 1993), Snyder (1966), Stotz *et al.* (1996), Todd (1943), Willard *et al.* (1991), Williams & Tobias (1994), Zimmer (1948).

## 25. Black-throated Trogon

### *Trogon rufus*

**French:** Trogon aurore **German:** Schwarzkehltrogon **Spanish:** Trogón Amarillo  
**Other common names:** Graceful Trogon, Yellow-bellied Trogon

**Taxonomy.** *Trogon rufus* J. F. Gmelin, 1788, Cayenne.

Possibly closest to *T. mexicanus*, *T. elegans*, *T. collaris*, *T. personatus* and *T. curucui*; DNA studies suggest that middle three of these may be nearest relatives. Six subspecies recognized.

#### Subspecies and Distribution.

*T. r. tenellus* Cabanis, 1862 - E Honduras, Nicaragua, both slopes of Costa Rica (except NW) and Panama, and extreme NW Colombia.

*T. r. cupreicauda* (Chapman, 1914) - W Colombia and W Ecuador.

*T. r. rufus* J. F. Gmelin, 1788 - E Venezuela and the Guianas to N Brazil (R Negro region and Amapá).

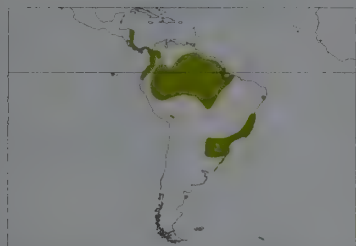
*T. r. sulphureus* Spix, 1824 - SE Colombia, E Ecuador, NE Peru and W Brazil.

*T. r. amazonicus* Todd, 1943 - NC Brazil (lower Amazon Valley).

*T. r. chrysocloros* Pelzel, 1856 - Paraguay, NE Argentina and E & SE Brazil (Bahia to Rio Grande do Sul, and including Mato Grosso); presumably this race in NE Brazil (Alagoas).

**Descriptive notes.** 23-25 cm; 48-57 g. Male nominate race with bill greenish-yellow, orbital ring pale blue; face and throat black; crown, breast and upperparts metallic olive-green; mid-breast to undertail-coverts rich yellow; uppertail metallic olive, tipped black; undertail evenly barred black and white, with broader tips forming 3 white bands. Female with black culmen, broken white eyering, coffee-brown head, breast and upperparts, duller yellow below, flanks washed brown; uppertail rufous, tipped black, undertail like male's but with broader white barring. Immature like respective adult but duller, undertail more coarsely barred, male has throat and breast largely brown. Race *tenellus* with turquoise-blue uppertail, and more golden-green overall than *cupreicauda*, with which it shares more boldly barred undertail than S races; *cupreicauda* with uppertail bronzy-green, female with outer tail feathers rufous-chestnut; *sulphureus* and *amazonicus* with uppertail coppery-gold and bronzy-green respectively; *chrysocloros* large, with finer vermiculations on





wingpanel and narrower white bars on undertail than *amazonicus*. **Voice.** Song a slowly delivered series of 2-5 clear, mellow, deliberate "cow" whistles, decreasing in pitch; when cautious or alarmed, a churring or rattling "krrr" or nasal "nyurrrrr".

**Habitat.** Inhabits understorey and mid-levels of humid lowland primary forest and adjacent tall second growth, sometimes cacao plantations or other semi-open woodland, edges and clearings with dark dense understorey; lowlands locally to 1100 m. At N end of range, in Honduras, seems to favour denser areas of coastal rainforest, being rare in second growth,

and not found above 400 m. In Amazon Basin, found in *terra firme* forest in Tambopata, Peru, and creekside forest in Amazonas, Brazil.

**Food and Feeding.** Possibly less frugivorous than most other Neotropical trogons; absence of regurgitated seeds in nest-bottoms suggests incubating birds much less dependent on vegetable material than are other species studied. However, berries, fruit and once even leaves have been found in stomachs. Insect diet includes beetles, various Orthoptera, mantises and caterpillars. Noted following ant swarms, troops of monkeys, and mixed-species flocks.

**Breeding.** Feb-Jun in Costa Rica, Feb-Jul in Panama; birds in breeding condition in Feb-May in Colombia; Mar in Venezuela, Oct in French Guiana. May in Brazil. Nest a shallow unlined niche that leaves most of sitting bird exposed, 0.75-6 m up in slender decaying stub, including palm, once

in dead branch of living tree; once in old termite nest. Eggs 2; incubation 18-19 days; nestling period 14-15 days. Age of maturity may be 2 years for male.

**Movements.** Generally resident. A record in Costa Rica from near Golfo de Nicoya was undoubtedly of a stray individual.

**Status and Conservation.** Not globally threatened. Uncommon to fairly common in limited range in Honduras; in Costa Rica, common on Caribbean slope (except in drier lowland areas) and S Pacific slope, less abundant towards Puntarenas; in Panama fairly common, generally more numerous on Caribbean side, except in E. Fairly common in Colombia, also in French Guiana (where less common than *T. viridis*). Uncommon in Amazonian Brazil, but present in Tapajós National Park, Pará; also in SE Brazil in Sooretama and Augusto Ruschi Biological Reserves, Espírito Santo, in Itatiaia and Serra dos Órgãos National Parks, Rio de Janeiro, and in Iguazu National Park, Paraná, but scarce farther S. Rare in Argentina (Misiones), although locally common in Iguazú National Park; generally uncommon or rare in E Paraguay, but nonetheless widespread; rare in Peru, and little known at Tambopata. Highly sensitive to logging, and likely to disappear from disturbed tracts.

**Bibliography.** Angehr & Christian (2000), Anon. (1998d), Belton (1984), Boinski & Scott (1988), Canevari *et al.* (1991), Carriker (1910), Chebez (1994), Donahue (1994), Dubs (1992), Friedmann (1948), Guix (1995), Gyldestolpe (1951), Haffer (1975), Haverschmidt & Meev (1994), Hilty & Brown (1986), Lowen *et al.* (1996), Meyer de Schauensee (1949), Meyer de Schauensee & Phelps (1978), Monroe (1968), Norton (1965), Oniki & Willis (1983), Oren & Parker (1997), Parker & Goerck (1997), Partridge (1954), de la Peña (1994), Peres & Whittaker (1991), Phelps & Phelps (1958), Pinto (1938, 1947, 1950), Ridgely & Gwynne (1989), do Rosário (1996), Ruschi (1979), Saibene *et al.* (1996), Salvin & Godman (1888-1904), Schubart *et al.* (1965), Short (1975), Sick (1985, 1993), Skutch (1959, 1983), Slud (1960, 1964), Stiles & Skutch (1989), Stotz *et al.* (1996), Teixeira *et al.* (1986), Thiollay (1992), Thiollay & Jullien (1998), Todd (1943), Tostain *et al.* (1992), Wetmore (1968), Zimmer (1930, 1948).



*ssp. surracura*

26

*ssp. aurantius*

27

*ssp. peruvianus*

*ssp. curucui*

29

*ssp. mexicanus*

*ssp. australis*

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*ssp. massena*

*ssp. melanurus*

*ssp. macroura*

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PLATE 6

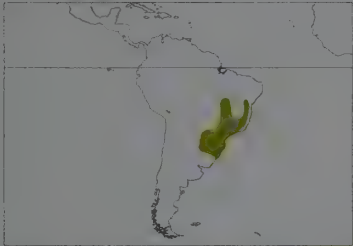
inches 5  
cm 13



26. Surucua Trogon  
*Trogon surrucura*

**French:** Trogon surucua      **German:** Surucuatrogon      **Spanish:** Trogón Surucúa  
**Other common names:** Orange-breasted(!)/Brazilian Trogon (*aurantius*)

**Taxonomy.** *Trogon surrucura* Vieillot, 1817, Paraguay.  
May possibly be related to the superspecies that includes *T. viridis*, *T. bairdii*, *T. citreolus* and *T. melanocephalus*. Race *aurantius* has sometimes been considered a separate species, but it intergrades with the nominate race in the Rio de Janeiro area of SE Brazil. Two subspecies currently recognized.  
**Subspecies and Distribution.**  
*T. s. aurantius* Spix, 1824 - EC & SE Brazil (S to N São Paulo).  
*T. s. surrucura* Vieillot, 1817 - E Paraguay and NE Argentina E to SE Brazil (Rio Grande do Sul); probably also S into Uruguay.



**Descriptive notes.** 26 cm; 73 g. Male of nominate race has bill greenish-grey, orbital ring orange; forehead, cheeks and throat blackish, rest of crown, neck and breast royal blue, often becoming more turquoise-blue on nape and at breastline; back coppery-green, shading to turquoise-green on tail; wingpanel very densely vermiculated (looking grey in field); belly pinkish-red, grey on flanks; undertail appears all-white with black terminal bar. Female dull grey, with tiny white spot before and behind eye, distinct but narrow white bars on wingpanel, black undertail, the three inner pairs of rectrices with white outer vanes and

terminal bars. Immature male has black tips to feathers of undertail, immature female similar to adult female. Race *aurantius* has orange belly and yellow orbital ring, female has whitish mid-belly. **Voice.** Song an ascending sequence of 14-17 full "diu" or "kwa" notes, final syllable lower, like *T. viridis*; warning "kiarr".

**Habitat.** Middle stratum of primary and tall secondary forest and semi-deciduous woodland, to c. 2000 m.

**Food and Feeding.** Diet consists of Lepidoptera larvae, Diptera (Brachycera), grasshoppers, spiders, cicadas, moths, tettigoniids, flying termites and ants; seeds in stomachs indicate some frugivory. Birds in flight recorded catching insects, both plucking them from branches and flycatching them in mid-air.

**Breeding.** Recorded Sept-Dec in SE Brazil (Rio Grande do Sul), Sept in Paraguay; excavation of sites from Aug in Argentina. Nest situated in termitarium or rotting tree, latter including introduced *Melia azederach*; also recorded in thick tree-fern trunk and in tall cactus. No other details known.

**Movements.** Apparently sedentary for the most part, but southernmost populations move N for austral winter.

**Status and Conservation.** Not globally threatened. In Brazil, present in Sooretama and Augusto Ruschi Biological Reserves, Espírito Santo, in Itatiaia and Serra dos Órgãos National Parks, Rio de Janeiro, in Iguaçu National Park, Paraná, and in Nonai and Turvo Forest Reserves, Rio Grande do Sul. In Argentina, present in Chaco and Río Pilcomayo National Park and El Bagual Reserve; common at Iguazú National Park and Uruguá-i Provincial Park. Generally common and widespread in E Paraguay.

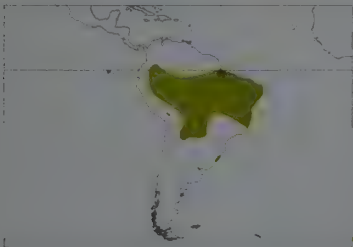
**Bibliography.** dos Anjos *et al.* (1997), Belton (1984), Brooks *et al.* (1993), Canevari *et al.* (1991), Capper *et al.* (2000), Contreras *et al.* (1990), Descourtiz (1983), Dubs (1992), Goerck (1999), Gonzaga *et al.* (1995), Guix (1995), López (1997), Lowen *et al.* (1996), Meyer de Schauensee (1982), Moojen *et al.* (1941), Parker & Goerck (1997), de la Peña (1994), Pinto (1935, 1938, 1950), do Rosário (1996), Ruschi (1979), Sathene *et al.* (1996), Schubart *et al.* (1965), Short (1975), Sick (1985, 1993), Stotz *et al.* (1996), Wetmore (1926).

27. Blue-crowned Trogon  
*Trogon curucui*

**French:** Trogon couroucou      **German:** Blauscheiteltrogon      **Spanish:** Trogón Curucuí

**Taxonomy.** *Trogon Curucui* Linnaeus, 1766, Mexico, Brazil, Peru = Brazil.  
Possibly closest to *T. mexicanus*, *T. elegans*, *T. collaris*, *T. personatus* and *T. rufus*; DNA studies suggest, however, that nearest relatives may be *T. violaceus* and *T. viridis*. Formerly current name *variegatus* is a junior synonym of *curucui*, whereas *bolivianus* is a synonym of *peruvianus*. Three subspecies recognized.

**Subspecies and Distribution.**  
*T. c. peruvianus* Swainson, 1838 - foot of E Andes from Colombia S to NW Bolivia (R Beni), and E to NC Brazil (R Tapajós).  
*T. c. curucui* Linnaeus, 1766 - C & E Brazil.  
*T. c. behni* Gould, 1875 - E Bolivia, SW Brazil, Paraguay and N Argentina.



**Descriptive notes.** 24 cm; 39-63 g. Male nominate race with bill yellow, orbital ring orange; forehead, face and throat blackish; rest of crown, sides of neck and breast glossy greenish-blue, turquoise-green on nape; upperparts metallic bronze-green, upptail greenish-blue; wingpanel very densely vermiculated (appearing grey in field); breastband white, underparts otherwise rosy-red; undertail black with narrow white bars and broader white tips. Female has yellow bill, strong broken white eyering, grey head, breast, upperparts and upptail, wingpanel with distinct white bars, white breastband with pinkish-red below, blackish undertail with white outer vanes (often black-notched) and terminal

bars. Race *peruvianus* has slight bluish gloss to upperparts, little or no white breastline, narrow white barring on undertail; *behni* slightly larger, possibly more bronze-backed with greener-tinged breast. **Voice.** Song like that of *T. viridis* or a slow version of Eurasian Wryneck (*Jynx torquilla*), but tends to accelerate throughout, then stop abruptly; also purring calls like congeners.

**Habitat.** Occupies a variety of habitats, mainly canopy, subcanopy and understorey of *várzea*, gallery and other river-margin forest, transition forest, tall second growth, monsoon forest, savanna woodland, dry semi-deciduous forest, dry palm forest, lake margins and forest openings, woodland edge and scrub; occurs up to at least 500 m, and probably higher. Reaches higher elevations in S half of range, occurring as high as 1750 m in Bolivia, and common in montane woodland to 1500 m in Argentina. In Formosa, Argentina, found in islands of dry forest formed by *Tabebuia*, *Celtis*, *Schinopsis*, *Prosopis*, etc. In Piauí, Brazil, recorded from buriti palm swamp vegetation and surrounding dry scrub forest (*mata seca*) and *caatinga* (bushy-arboreal and arboreal).

**Food and Feeding.** Diet consists principally of insects, with typical items including hairy caterpillars, Orthoptera (grasshoppers and bush-crickets), beetles (Chrysomelidae, Alleculidae), dragonflies (Anisoptera), Hemiptera (Reduviidae), stick-insects (Bacteriidae), mantises, Homoptera (cicadas) and wasps, as well as spiders; also various small fruits (e.g. Lauraceae). Joins mixed-species flocks.

**Breeding.** Recorded May in Colombia, Jul in Peru; Sept in Mato Grosso, Jul in Pará, Brazil; Oct in Bolivia, Oct-Dec in NE Argentina. Nest situated in termitarium; in one case reported, the birds used a nest of *Nasutitermes corniger* 2-3 m above ground in a citrus tree; another 5 m up a tree, with entrance 6.5 x 7 cm, passing down a tunnel 15 cm long to a chamber 10-12 cm in diameter; other known nests located 0.5-4 m above ground. Clutch 2-3 eggs. No further information available.

**Movements.** Apparently sedentary.  
**Status and Conservation.** Not globally threatened. Uncommon in Colombia; fairly common in Peru, where in floodplain-forest measured territories c.7 ha, with as many as 8-5 pairs/km², but uncommon at Tambopata. Present in Bolivia in Beni Biological Station and in Madi, Ambooró and Noel Kempff Mercado National Parks; common in subtropical zone of Chuquisaca and Tarija. In Argentina, common in El Rey National Park (Salta), and present in Calilegua and Río Pilcomayo National Parks. In Brazil, fairly common in Serra da Capivara National Park, Piauí, and present in Tapajós National Park, Pará.

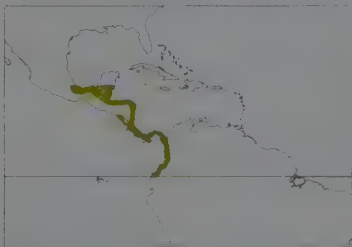
**Bibliography.** Babarskas *et al.* (1995), Brightsmith (1999), Canevari *et al.* (1991), Chebez *et al.* (1999), Davis (1993), Di Giacomo & López (1998), Donahue (1994), Dubs (1992), Eistenraut (1935), Fjeldsá & Mayer (1996), Gil *et al.* (1990), Griscom & Greenway (1941), Gyldestolpe (1951), Hilty & Brown (1986), Hoy (1968), López (1997), Meyer de Schauensee (1949), Novaes (1992), Olmos (1993), Oren & Parker (1997), Pearman (1993), de la Peña (1994), Perry *et al.* (1997), Pinto (1935, 1938, 1950), Rensen & Traylor (1989), Ruschi (1979), Schubart *et al.* (1965), Short (1975), Sick (1985, 1993), Sneath (1927-1928), Stotz *et al.* (1996), Terborgh *et al.* (1990), Wetmore (1926), Zimmer (1948).

28. Slaty-tailed Trogon  
*Trogon massena*

**French:** Trogon de Masséna      **German:** Schieferschwanztrogon      **Spanish:** Trogón Grande  
**Other common names:** Massena Trogon; Chapman's Trogon (*australis*)

**Taxonomy.** *Trogon massena* Gould, 1838, Mexico.  
Perhaps most closely related to *T. melanurus*, *T. clathratus* and *T. comptus*. Race *australis* sometimes placed with *T. melanurus*; alternatively, when race *macroura* of latter is treated as full species, *australis* is sometimes considered a race of that. Race *hoffmanni* intergrades with nominate in N and with *australis* in S; this race is not well defined and possibly invalid. Three subspecies tentatively recognized.

**Subspecies and Distribution.**  
*T. m. massena* Gould, 1838 - Caribbean slope of SE Mexico (E from Veracruz), Belize, N Guatemala, N Honduras, and both slopes in Nicaragua.  
*T. m. hoffmanni* (Cabanis & Heine, 1863) - Costa Rica (not dry NW) and Panama.  
*T. m. australis* (Chapman, 1915) - W Colombia and NW Ecuador.



**Descriptive notes.** 33-35 cm; 141 g. Male nominate race with stout orange-red bill, orange-red orbital ring; face and throat blackish; crown, nape, upperparts and breast green, belly to undertail-coverts red; vermiculated wingpanel; rump and upptail-coverts green to turquoise, upptail greenish with golden gloss, undertail slaty. Distinguished from *T. mexicanus* by much larger size, larger and orange-red bill, whitish on primaries, lack of white breastband, and colour and pattern of tail. Female slaty on upper mandible, head, upperparts, wings and tail, fading to paler slaty from throat to mid-belly, red lower belly to

undertail-coverts. Immature male like adult male above, like female below, undertail with whitish tips and notching on outer webs; immature female like adult female, but tail as immature male. Race *australis* male with central tail feathers bluish, instead of green; *hoffmanni* similar to *australis* but averages smaller, and has tail more golden. **Voice.** Song a steady nasal barking, "koh koh koh koh koh", lower-pitched and slower than *T. viridis*; calls include quiet clucks and a hard chatter.

**Habitat.** Canopy and middle levels of dense humid and wet lowland and foothill evergreen forest, forest edge, second-growth woodland and mangroves, sometimes coffee groves and small patches of forest inside plantations, coming lower at edges and adjacent semi-open or second growth; sometimes ventures short distances into patches of secondary woodland and clearings with scattered trees to forage or search for nest-sites. To 500 m in Guatemala, 800 m in Belize, 300 m in Honduras; locally in Costa Rica to 1200 m.

**Food and Feeding.** Various fruits, including *Coussarea*, *Hamelia*, *Guatteria*, *Virola sebifera* and *V. surinamensis*, and small palms; also caterpillars (including sphingids), beetles (including cerambycids), Orthoptera, other insects, and small lizards. Sallies from perch to grab fruit or to snatch prey from foliage. May follow monkey troops or cacique (*Cacicus*) flocks, catching insects flushed by them.

**Breeding.** Apr-Jun in Mexico, Mar-Jun in Belize, Feb-Jul in Costa Rica and Panama; birds in breeding condition in Feb in Colombia (Chocó). Nest an unlined chamber with ascending entrance tunnel, carved by both sexes, 2.5-15 m up in termitary or rotten trunk; once attempted in crown of introduced oil palm (*Elaeis guineensis*). Eggs 3. No information on incubation and nestling periods.

**Movements.** Largely resident; some movement occurs, however, with birds reaching Pacific slope through passes in Cordillera de Guanacaste, in NW Costa Rica.

**Status and Conservation.** Not globally threatened. Fairly common to common throughout most of range. In Mexico, fairly common in Oaxaca and Yucatán; fairly common in Guatemala in 1960's, where present in Tikal National Park; moderately common in Belize; uncommon to fairly common in Honduras. In Costa Rica, a common resident in S Pacific and Caribbean lowlands and foothills, but rare in drier lowlands W of Upala (Caribbean side). Fairly common to common in Panama, where especially widespread and numerous on Caribbean side of Canal area. Uncommon in Munchique National Park, Colombia.

**Bibliography.** Aldrich & Bole (1937), Alvarez del Toro (1980), Anon. (1998d), Binford (1989), Brodkorb (1943), Carraker (1910), Fogden (1993), González-García (1993), Halfer (1975), Hilty & Brown (1986), Howe (1982), Howell, S.N.G. & Webb (1995), Howell, T.R. (1957), Kennard & Peters (1928), Land (1970), Lowery & Dalquest (1951), Meyer de Schauensee (1949, 1982), Miller (1995), Moermond & Santana (1984), Monroe (1968), Paynter (1955), Ridgely & Gwynne (1989), Russell (1964), Santana *et al.* (1986), Skutch (1953, 1972a, 1999), Slud (1960, 1964), Smithe (1966), Stiles & Skutch (1989), Stott & Selsor (1961), Stotz *et al.* (1996), Valley & Whitman (1997), Van Tine (1935), Wetmore (1968), Willis & Eisenmann (1979).

## 29. Black-tailed Trogon

### *Trogon melanurus*

**French:** Trogon à queue noire **German:** Schwarzschwanztrogon **Spanish:** Trogón Colinegro  
**Other common names:** Large-tailed Trogon (*macroura*)

**Taxonomy.** *Trogon melanurus* Swainson, 1838, Demerara (= Georgetown), Guyana. Closest relatives may be *T. massena*, *T. clathratus* and *T. comptus*. Probably forms a parapatric species pair with *T. comptus*. Present species sometimes thought to include race *australis* of *T. massena*. Race *macroura* sometimes suggested to be a distinct species, and *T. massena australis* then regarded by some authors as belonging therein. Birds from Amazonian Brazil sometimes separated as race *occidentalis*. Four subspecies currently recognized.

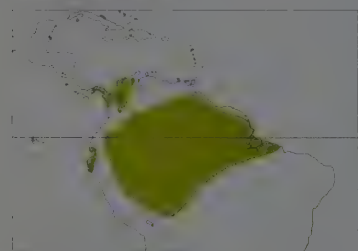
#### **Subspecies and Distribution.**

*T. m. macroura* Gould, 1838 - C Panama (E of Canal Zone) to N Colombia and extreme NW Venezuela.

*T. m. mesurus* (Cabanis & Heine, 1863) - W Ecuador and NW Peru.

*T. m. melanurus* Swainson, 1838 - E of Andes from Colombia E through Venezuela to the Guianas and NE Brazil (Maranhão).

*T. m. eumorphus* Zimmer, 1948 - Amazon Basin from E Ecuador and Peru E to NC Brazil (to E of Manaus), S to N Bolivia.



**Descriptive notes.** 28-30 cm; 52-122 g. Male nominate race with yellow bill, orange-red orbital ring; face and throat blackish; crown, nape, upperparts and breast green; white breastband, red belly to undertail-coverts; vermiculated wingpanel; uppertail deep blue, sometimes somewhat greener, undertail slaty. Differs from very similar *T. massena* in bill colour and white breastband. Female with slaty upper mandible, dark slaty head, upperparts, wings and tail, paler on throat to mid-belly, with red lower belly to undertail-coverts; differs from female *T. massena* in yellow lower mandible. Race *macroura* has larger bill.

longer wings and tail, and more turquoise on uppertail-coverts; *mesurus* has pale irides; *eumorphus* darker wings, bluer tail and narrower breastband. **VOICE.** Calls very like those of *T. massena*, but notes louder, more resonant, perhaps given faster, "kwo-kwo-kwo..." in series of up to 25 notes; also a bubbly purring trill.

**Habitat.** Humid lowland and foothill forest, forest edge and second-growth woodland on both slopes in Panama, penetrating mangroves on Caribbean side; in Colombia reaches 2200 m (usually much lower) W of Andes, to 500 m E of Andes, and persists in small patches of forest in generally cleared areas in NW Colombia. In Venezuela occupies rainforest to elevation of 100 m N of Orinoco, to 1000 m S of it; in French Guiana mainly in primary forest in interior. In Amazonia found in canopy and subcanopy of poorly drained transition forest and swamp-forest, forest edge and gallery forest; sometimes alongside *Pharomachrus pavoninus* and *T. collaris*.

**Food and Feeding.** Berries, palm and other fruits, *Cecropia* flower tassels, also insects including Orthoptera (locustids), Coleoptera (cerambycids, curculionids), stick-insects and occasional caterpillars. Follows mixed-species flocks in canopy.

**Breeding.** Mar in Panama; in Colombia, birds in breeding condition in Jan-May, nest excavation in Mar; Jul-Oct in French Guiana, Sept-Oct in Peru; Jun-Jul in Amazonia. All documented nests in Peru in active termitaria of *Nasutitermes corniger* (all of them already housing colonies of *Dolichoderus* ants), chiefly in mature or late successional floodplain-forest, and mostly in *Scheedia* or *Astrocaryum* palms; occasionally nests in hole in tree. Eggs 2-3. No other details known.

**Movements.** Largely resident; in Bolivia, birds move from dry forest in wet season to lowland rainforest in dry season.

**Status and Conservation.** Not globally threatened. Uncommon and rather local in Canal area, Panama, but more numerous in E lowlands. In Colombia, common in lower Atrato Valley and E of Andes, and fairly common generally in NW; abundant in Las Orquídeas National Park. Widely distributed and not uncommon in interior Surinam. Present in Bolivia in Beni Biological Station and in Madidi, Amoró and Noel Kempff Mercado National Parks. In Brazil, common in Amazonia; and present in Tapajós National Park, Pará. In Peru uncommon at Tambopata, but in floodplain-forest territory c. 5 ha and as many as 13 pairs/km<sup>2</sup>; common in Manu area; rare in arid tropical zone.

**Bibliography.** Anon. (1998d), Best & Clarke (1991), Brightsmith (1999, 2000), Cohn-Haft *et al.* (1997), Donahue (1994), Echeverri (1986), Foster *et al.* (1994), Friedmann (1948), Gyldestolpe (1945a, 1945b, 1951), Halfer (1967a, 1967b, 1975), Haverschmidt & Mees (1994), Hilty & Brown (1986), Meyer de Schauensee (1949, 1982), Meyer de Schauensee & Phelps (1978), Oren & Parker (1997), Parker *et al.* (1982), Perry *et al.* (1997), Phelps & Phelps (1958), Pinto (1938, 1947, 1950), Pople *et al.* (1997), Remsen & T aylor (1989), Ridgely & Gwynne

(1989), Ruschi (1979), Schubart *et al.* (1965), Sick (1985, 1993), Snyder (1966), Stotz *et al.* (1996), Terborgh *et al.* (1990), Thiollay & Jullien (1998), Todd (1943), Tostain *et al.* (1992), Wetmore (1968), Williams & Tobias (1994), Willis & Eisenmann (1979), Zimmer (1948).

## 30. Lattice-tailed Trogon

### *Trogon clathratus*

**French:** Trogon échelette **German:** Sperberschwanztrogon **Spanish:** Trogón Colibarrado

**Taxonomy.** *Trogon clathratus* Salvin, 1866, Santa Fé de Veragua, Panama.

Closest relatives possibly *T. massena*, *T. melanurus* and *T. comptus*. Monotypic.

**Distribution.** Caribbean slope from Costa Rica to W Panama, where locally also on Pacific slope.



**Descriptive notes.** 30 cm; 130 g. Male has yellow bill and whitish iris; face and throat blackish; crown, nape, upperparts and breast green, belly to undertail-coverts rosy-red; vermiculated wingpanel; uppertail bluish-green, undertail looks slaty with well-spaced thin white bars. Differs from very similar *T. massena* in bill and eye colours, rosier belly, bluer tail, undertail pattern. Female has dark upper mandible, slaty crown and upperparts, olive-slate breast; differs from *T. massena* in breast colour, rosier belly, yellow lower mandible, undertail barring is nearly restricted to outer webs, distinct white tips to feathers of

undertail. Immature like respective adult, but rectrices more pointed and more coarsely barred, breast of male largely brown. **VOICE.** A rapid series of c.15 loud, resonant clucking "kwa" notes rising in pitch and volume to a crescendo in middle, then becoming faster, lower and softer; clearer, higher-pitched, less nasal and more patterned than *T. massena*.

**Habitat.** Lower canopy and middle levels of humid and wet forest in foothills and on lower mountain slopes, at 90-1360 m, barely ever in level lowlands; sometimes comes to edge or into adjacent shaded semi-open areas. Centre of abundance follows foothills and slopes of the cordilleran core of Costa Rica. Favours more humid areas, especially hilly or lower montane, than more numerous sympatric *T. massena*, and is more restricted to tall undisturbed forest.

**Food and Feeding.** Various Lauraceae and other fruits, also large insects, and occasionally small frogs and lizards.

**Breeding.** Recorded Feb-May. Nest is a cavity in a rotting stub or snag, occasionally an arboreal termitarium, situated 5-8 m above ground. Eggs, and incubation and nestling periods, apparently undocumented.

**Movements.** Descends from higher parts of range in middle to late rainy season.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in Central American Caribbean Slope EBA. Uncommon to fairly common in Costa Rica; apparently rare, although perhaps overlooked, in Panama. Habitat destruction within its range now extensive, however, and careful evaluation of status needed.

**Bibliography.** Anon. (1998d), Blake & Loiselle (2000), Engleman (1996b, 1996c), Fogden (1993), Pearman (1995), Ridgely & Gwynne (1989), Slud (1960, 1964), Stattersfield *et al.* (1998), Stiles (1985), Stiles & Skutch (1989), Stotz *et al.* (1996), Wetmore (1968).

## 31. White-eyed Trogon

### *Trogon comptus*

**French:** Trogon aux yeux blancs **German:** Blauschwanztrogon **Spanish:** Trogón Coliazul  
**Other common names:** Blue-tailed Trogon(!)

**Taxonomy.** *Trogon comptus* Zimmer, 1948, Bahía de Málaga, Colombia.

Closest relatives possibly *T. massena*, *T. melanurus* and *T. clathratus*. Probably forms a parapatric species pair with *T. melanurus*. Superficial similarity to both *T. massena* and *T. melanurus*, combined with extensive sympatry, has led some authors to suggest that present species might perhaps be conspecific with some form currently placed within one or other of these two. Monotypic.

**Distribution.** W Colombia and NW Ecuador.



**Descriptive notes.** 28 cm; 104 g. Male with yellow bill, white iris; face and throat blackish; crown to back, and breast, green with slight bluish tinge, rump and tail purplish-blue, tail broadly tipped black; vermiculated wingpanel; belly to undertail-coverts red; undertail slaty. Differs from *T. massena* in smaller size, shorter tail, bill and eye colours, no conspicuous orbital ring, bluish tinge to green of plumage, rump and tail colour. Female with slaty upper mandible, head, upperparts, wings and tail, grey breast to mid-belly, red lower belly to undertail-coverts; differs from female *T. massena* in white iris,

yellow lower mandible, darker grey breast. **VOICE.** Song very similar to that of *T. melanurus*, but notes slightly lower and more widely spaced.

**Habitat.** Humid and wet forest and forest borders, favouring foothills and broken hilly terrain, from sea-level to 1800 m; once recorded in forest along riverbanks formed by slopes and 60-m sandstone bluffs.

**Food and Feeding.** No information.

**Breeding.** Birds in breeding condition in Mar. No other details known.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in Nechí Lowlands EBA and Chocó EBA. Usually less numerous than *T. massena*, with which it sometimes occurs. In one study, singing males were spaced several hundred metres apart along banks of R Bojayá, NW Colombia.

**Bibliography.** Best *et al.* (1997), Butler (1979), Halfer (1967a, 1975), Hilty & Brown (1986), Meyer de Schauensee (1949, 1982), Pople *et al.* (1997), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Taylor (1995), Zimmer (1948).



Genus *PRIOTELUS* G. R. Gray, 1840

32. Cuban Trogon

*Priotelus temnurus*

**French:** Trogon de Cuba      **German:** Kubatrogon      **Spanish:** Trogón Toco-ro

**Taxonomy.** *Trogon temnurus* Temminck, 1825. Havana, Cuba. Populations on cays off N Cuba may merit treatment as distinct subspecies. Two subspecies currently recognized.  
**Subspecies and Distribution.**  
*P. t. temnurus* (Temminck, 1825) - Cuba, including large cays N of Camagüey Province (Romano, Guajaba and Sabinal).  
*P. t. vescus* (Bangs & Zappey, 1905) - I of Pines.



**Descriptive notes.** 23-25 cm; 58 g. Male nominate race with bill reddish-pink, darker on culmen, face blackish with reddish iris, crown and nape dull violet-blue; malar region, sides of neck and chin white, throat and breast greyish-white, belly to undertail-coverts red; mantle to rump green, with large white spots on coverts and regular white notches on outer webs of primaries; uppertail dark green-blue, central pair of feathers with inner webs bronze-blue, tips excised; undertail with three outer pairs of feathers basally blackish with white notches on outer webs, distally white with excised tips creating distinctive ragged white "thorns" down outer edge. Female like male. Race *vescus* very slightly smaller (no overlap in wing length). **VOICE.** Varied: song a pleasant "toco-toco-tocoro-tocoro...", repeated at intervals and for long periods, sometimes with female responding; calls include a low short mournful note, difficult to locate.

**Habitat.** Occurs in wet and dry forest, shrubbery and copses near streams and rivers, within these habitats generally keeping to shady areas; found at all altitudes, but is most numerous in montane habitat.

**Food and Feeding.** Feeds mainly on flowers, but also takes buds, fruits (including oranges) and insects. Hovers while feeding, like a tyrant-flycatcher (Tyrannidae).

**Breeding.** Primarily May-Aug. Nest commonly in abandoned hole of woodpecker or in natural cavity. Eggs 3-4. No details of incubation and fledging periods.

**Movements.** Apparently sedentary.

**Status and Conservation.** Not globally threatened. Considered common and widespread throughout Cuba, but rare on Guajaba, Romano and Sabinal; formerly common in S part of I of Pines, but has now apparently become uncommon. Present in Reserva Natural de Cupeyal. The national bird of Cuba.

**Bibliography.** Alayón (1987), Anon. (1998d), Bangs & Zappey (1905), Barbour (1923, 1943), Bond (1956, 1985), Chapman (1902), Clark (1918), Díaz (1999), García (1980, 1987), Garrido (1980), Garrido & Kirkconnell (2000), Garrido *et al.* (1986), González-Alonso *et al.* (1992), Gundlach (1873), Hernández *et al.* (1999), Morales & Garrido

(1996), Raffaele *et al.* (1998), Rinke (1997), Rutgers & Norris (1977), Rutten (1934), Stotz *et al.* (1996), Sulley & Sulley (1992), Todd (1916), Vaurie (1957).

Genus *TEMNOTROGON* Bonaparte, 1854

33. Hispaniolan Trogon

*Temnotrogon roseigaster*

**French:** Trogon damoiseau      **German:** Rosentrogon      **Spanish:** Trogón de la Española

**Taxonomy.** *Trogon roseigaster*, Vieillot, 1817, Santo Domingo. Often placed in genus *Priotelus*, but shows significant differences from *P. temnurus* in bill pattern, plumage coloration and some morphological features. Monotypic.  
**Distribution.** Hispaniola.



**Descriptive notes.** 27-30 cm; 74 g. Male with bill yellow, mask blackish with orange eye, crown and upperparts green, with distinct white bars on wingpanel and regular white notches on outer webs of primaries; chin, throat, breast and upper belly grey, lower belly to undertail-coverts red; uppertail green-blue, central pair of feathers with inner webs dull grey-bronze; undertail looks mostly black with very broad white tips. Female lacks white notches on primaries, has wingpanel unbarred grey-green, less vivid red belly. **VOICE.** Song "kuh kwao", "kuh kwao kwao", "toca-loro" or "cock-craow", repeated several times together; calls

include puppy-like barking when disturbed, a low rattle and whimpering whistles.

**Habitat.** Mountain forest, including mature pine and deciduous broadleaf forest, above 300 m; also locally or occasionally in coastal mangroves. Dependent on large mature trees for nesting cavities.

**Food and Feeding.** Diet consists mainly of insects; also small lizards, and fruits (those of the "parrot tree" being preferred).

**Breeding.** Mar-Jul. Nest in stub or tree cavity, often abandoned nest of Hispaniolan Woodpecker (*Melanerpes striatus*). Eggs 2. No other information available.

**Movements.** Descends to lower elevations in non-breeding season.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Restricted-range species: present in Hispaniola EBA. Formerly common in higher mountains, particularly in rainforest; only very local in lowlands. Still locally common in undisturbed habitat in Dominican Republic, e.g. in Sierra de Bahoruco National Park; still abundant in parts of Haiti (Massif de la Hotte) but declining overall and considered threatened there. Habitat destruction has caused considerable decline throughout species' range, and it is sometimes hunted for food.

**Bibliography.** Anon. (1998d), Bond (1928, 1956, 1985), Dod (1981, 1987, 1992), Latta & Wunderle (1996a), Raffaele *et al.* (1998), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wetmore & Swales (1931).





## Genus *EUPTILOLOTIS* Gould, 1858

### 34. Eared Quetzal

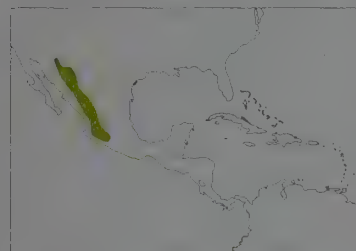
#### *Euptilotis neoxenus*

**French:** Trogon oreillard **German:** Haarbüscheltrogon **Spanish:** Trogón Orejón  
**Other common names:** Eared Trogon

**Taxonomy.** *Trogon neoxenus* Gould, 1838, Mexico.

Probably most closely related to *Priotelus* and *Tennotrogon*. Monotypic.

**Distribution.** SC USA (S Arizona) and W Mexico (Sierra Madre Occidental).



described as a "ka-ka-kak".

**Habitat.** Upper and middle storeys of primary but also disturbed and logged pine, pine-oak and pine-evergreen forest, particularly along watercourses in canyons ("canyon forest"), generally at 1800-3000 m and chiefly 2100-2800 m. Elevations possibly lower in N of range than in S. On Sonora-Chihuahua border, habitat at one site was open park woodland of *Pinus engelmanni*, *P. ponderosa* and *P. leiophylla* intermixed with *Quercus grisea*, at another *P. durangensis* and *Q. oblongifolia*; elsewhere dominant trees have included epiphyte-laden *Quercus*, *Abies* and *Magnolia*. In Arizona, the xeric vegetation comprises oak, cypress, sycamore (*Platanus*) and madroña (*Arbutus*). Nests tend to be situated in riparian corridors where habitat generally intact. In winter in Mexico, may penetrate lush subtropical and even tropical evergreen vegetation in barrancas and canyons.

**Food and Feeding.** Insects, including moths, and fruit, including the berry-like fruits of madroña (*Arbutus arizonica*). Most food taken in Nov in Arizona was madroña fruit. Caterpillars and beetles reportedly fed to young.

**Breeding.** Pairing Apr-Jun; breeds Jun-Oct, but records also in Apr, and even an immature with unossified skull from mid-Apr. Nest in tree cavity, e.g. old hole of Acorn Woodpecker (*Melanerpes formicivorus*) suffices; recorded in dead pine and maple, and such trees need not be large. No information on eggs and on incubation and fledging periods.

**Movements.** Mainly resident; population in S USA may be resident or seasonal. Less sedentary than many other trogons, pairs and groups moving readily through open woods, or across canyons. After becoming independent, young may wander, particularly to lower altitudes; moreover, species may more generally exhibit sporadic autumn/winter displacements to lower altitudes.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. At start of 1990's there were few known Mexican sites for this species, with La Michilía Biosphere Reserve, in Durango, perhaps the most important, and it was considered rare, classed as Endangered in 1994; main threat identified was logging and the removal of potential nest-site trees, which have been major causes of decline also of Thick-billed Parrot (*Rhynchopsitta pachyrhyncha*) and presumed extinction of Imperial Woodpecker (*Campephilus imperialis*). In 1995, however, a year's fieldwork in the Sierra Madre in search of the latter resulted in records of present species from 55 sites, and the quetzal was judged to be common in appropriate habitat, little affected by logging, and no longer in need of threatened status. In S Arizona, USA, first recorded in 1977, in autumn and winter, with first recorded breeding in 1991.

**Bibliography.** Anon. (1998d), Baicich & Harrison (1997), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Gonzaga *et al.* (1992), Howell & Webb (1995), Kaufman (1996), Lammertink (1996), Lammertink *et al.* (1997), Marshall (1957), Miller *et al.* (1957), Mlodinow & O'Brien (1996), van Rossem (1945), Salvin & Godman (1888-1904), Stotz *et al.* (1996), Taylor (1978a, 1994), Wege & Long (1995), Williamson (1992), Zimmerman (1978).

## Genus *PHAROMACHRUS* de la Llave, 1832

### 35. Pavonine Quetzal

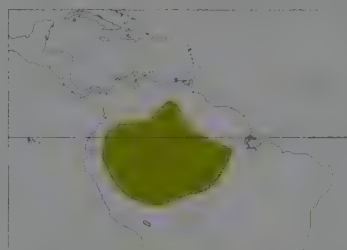
#### *Pharomachrus pavoninus*

**French:** Quetzal pavonin **German:** Pfauentrogon **Spanish:** Quetzal Pavonino  
**Other common names:** Pavonine Trogon

**Taxonomy.** *Trogon pavoninus* Spix, 1824, Rio Negro, Amazonas, Brazil.

Forms a superspecies with *P. auriceps*, with which may be conspecific; *P. fulgidus* possibly belongs to same superspecies. Population in the lower Amazon proposed as race *viridiceps*, but differences appear to be result of individual variation. Monotypic.

**Distribution.** E Ecuador, SE Colombia and NE Peru to S & E Venezuela (S Amazonas, Bolívar) and to C Amazon Valley in Brazil (N to upper R Negro, E to R Tapajós), S to N Bolivia.



**Descriptive notes.** 33-34 cm; 158 g. Male has bill with variable amount of orange-red, usually at least around base, yellow (towards tip (tip sometimes darker); golden-green head, metallic emerald-green upperparts and upper breast, red lower breast to undertail-coverts; elongate wing-coverts and uppertail-coverts, latter reaching tip of tail; undertail black. Very similar to *P. auriceps*, but averages slightly smaller, differs in bill colour, and head less golden, with feathers of head and throat shorter. Female duller than male, bill blackish with variable amount of red, usually at least around base, often much more; breast brownish, greyish-white on outer webs and tips; differs from female *P. auriceps* in bill colour, tone of head and breast, and undertail pattern. VOICE. Song apparently a sequence of 5 melodious notes, "ew ewwo-ewwo-ewwo-ewwo"; call a loud descending whistle followed by emphatic note, "heeeecar, chok!".

undertail with outer 3 feathers notched and barred

**Habitat.** Middle storey, canopy and sometimes edge of well-drained tall humid lowland *terra firme* forest, and poorly drained transition forest, to 700 m.

**Food and Feeding.** No information on foods. Sometimes joins mixed-species flocks.

**Breeding.** In Amazonas, in Feb. apparent nest in hole 9 m up in snag in forest. In area of R Sucusari, Loreto (NE Peru), full-grown chick seen in nest, mid-Jul; nest was hole c. 5 m up trunk of dead tree.

**Movements.** No information.

**Status and Conservation.** Not globally threatened. Poorly known. Uncommon and perhaps local in Colombia. Uncommon to rare, but shy and perhaps somewhat overlooked, in Peru, e.g. uncommon at Tambopata and Manu and around Iquitos.

**Bibliography.** Butler (1979), Chapman (1931), Descourtilz (1983), Donahue (1994), Friedmann (1948), Gyldestolpe (1945a, 1945b, 1951), Hilty & Brown (1986), Meyer de Schauensee (1949, 1982), Meyer de Schauensee & Phelps (1978), Miller (1963), Oniki & Willis (1982), Parker *et al.* (1982), Peres & Whittaker (1991), Phelps & Phelps (1958), Pinto (1938, 1950), Remsen & Traylor (1989), Ruschi (1979), Salaman *et al.* (1999), Sick (1985, 1993), Stotz *et al.* (1996), Zimmer (1948).

### 36. Golden-headed Quetzal

#### *Pharomachrus auriceps*

**French:** Quetzal doré **German:** Goldkopftrogon **Spanish:** Quetzal Cabecidorado  
**Other common names:** Golden-headed Trogon

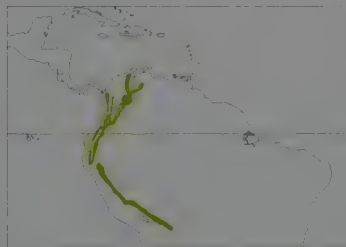
**Taxonomy.** *Trogon (Calurus) auriceps* Gould, 1842, Quito, Ecuador.

Forms a superspecies with *P. pavoninus*, and the two may be conspecific; *P. fulgidus* possibly belongs to same superspecies. Birds from NE Colombia currently placed in nominate race, but sometimes included in *hargitti*; population of W Ecuador described as race *heliactin*, but apparently inseparable from nominate. Two subspecies recognized.

**Subspecies and Distribution.**

*P. a. auriceps* (Gould, 1842) - E Panama (Cerro Pirre), and Andes from Colombia S to E Peru and N Bolivia.

*P. a. hargitti* (Oustalet, 1891) - Andes of Venezuela.



**Descriptive notes.** 33-36 cm, with male's tail plumes up to 8-10 cm more. Male of nominate race has yellow bill, gold-bronze head, metallic golden-green upperparts and breast, red lower breast to undertail-coverts; depending on angle of light, upperparts sometimes appear bluish; elongate wing-coverts and uppertail-coverts, latter reaching past tip of tail; undertail black. Differs most notably from *P. pavoninus* in coloration of bill and head. Differs from very similar *P. antisianus* in gold-bronze head uncrested at front, black undertail. Female with head and breast brownish, bill brownish or greyish, tail-coverts shorter, undertail with vestigial greyish-white tips; differs from female *P. antisianus* in unbarred undertail. Immature has pale edges also on secondaries and some vague pale mottling at tips of outer (shortest) tail feathers. Race *hargitti* longer-tailed, slightly more golden-sheened. VOICE. Melodic, mournful, far-carrying, hawk-like whistles, repeated 6-8 times, "whe-wheeu, whe-wheuu, whe-wheuu..."; other calls include rapid whinnying "why-dy-dy-dy-dyrrr", "hoo-whoooooo", and plaintive, guttural "ka-kaaaa".

**Habitat.** Inhabits humid and wet mid-elevation montane and foothill forest, less frequently forest edge and clearings, also tall second growth, and sometimes temperate cloudforest and elfin forest. Cloudforest on Cerro Pirre, in Panama, at 1200-1500 m; 1250-2600 m in Podocarpus National Park, Ecuador. In Venezuela, subtropical cloudforest and dwarf forest, in open terrain with scattered trees, at 2000-3100 m. Found on open hill-sides in early morning, retreating to forest during the day.

**Food and Feeding.** Fruits, frequently *Cecropia*, *Ocotea calophylla* and *Ficus*, especially *F. cundinamarensis*.

**Breeding.** Female seen in tree hole in Mar in Colombia; 4 nests close together in May in Ecuador. No further information available.

**Movements.** No information.

**Status and Conservation.** Not globally threatened. Fairly common throughout its range, including Panama. In Colombia, rare in Los Nevados National Park and uncommon in Munchie National Park; in Ecuador, the commonest trogon in the subtropical zone in Pichincha, and present in Podocarpus National Park; uncommon to fairly common in Peru.

**Bibliography.** Allen (1998), Anon. (1998d), Berry (1986), Best & Clarke (1991), Bloch *et al.* (1991), Butler (1979), Carrón (1986), Ejelds & Krabbe (1990), Goodfellow (1902), Hilty (1985), Hilty & Brown (1986), Hornbuckle (1999), Meyer de Schauensee (1949, 1982), Meyer de Schauensee & Phelps (1978), Parker *et al.* (1982), Rasmussen *et al.* (1994), Remsen & Traylor (1989), Ridgely & Gaulin (1980), Ridgely & Gwynne (1989), Rudloff (1992), Salaman *et al.* (1999), Stotz *et al.* (1996), Wetmore (1968), Williams & Tobias (1994), Zimmer (1948).



## 37. White-tipped Quetzal

*Pharomachrus fulgidus*

French: Quetzal brillant

German: Glanztrogon

Spanish: Quetzal Fúlgido

Other common names: White-tipped Trogon

**Taxonomy.** *Trogon fulgidus* Gould, 1838, Guiana? = northern Venezuela.May form a superspecies either with *P. pavoninus* and *P. auriceps* or with *P. antisianus* and *P. mocinno*. Two subspecies recognized.**Subspecies and Distribution.***P. f. festatus* Bangs, 1899 - N Colombia in Sierra Nevada de Santa Marta and adjacent areas.*P. f. fulgidus* (Gould, 1838) - N Venezuela.**Descriptive notes.** 33 cm. Male of nominate race has yellow bill, bronzy golden-green head with very small frontal crest, glossy emerald-green upperparts and breast, red lower breast to undertail-coverts; elongate wing-coverts and upptail-coverts, latter reaching past tip of tail; undertail black with broad white tips on 3 outer pairs of rectrices. Distinguished from very similar *P. auriceps* by undertail pattern, bronzy crown and nape clearly delimited from face and back, less blue tinge to green of plumage, red of belly perhaps extending higher up. Female duller, with darker bill; differs from female *P. antisianus* in bronzy-green crown,greener breast, far less red on underparts, and more white in tail. Immature male like female but with adult male undertail. Race *festatus* has longer, slightly more golden upptail-coverts. Voice. Calls a loud "kirra" or "kirra, kip", and variable "kieer, kip-kip-kip-a".**Habitat.** Middle levels and canopy of humid forest, cloudforest, borders, clearings, second-growth woodland, and moist ravines with coffee plantations; 1500-2500 m in Colombia, 900-1900 m in Venezuela.**Food and Feeding.** Fruits and berries. Observed sallying to pluck fruit from trees.**Breeding.** Birds in breeding condition in Jan-Apr; nest-cavities located in Mar and Aug. Nest in dead stub, trunk or limb, sometimes in old woodpecker hole, 4-10 m up.**Movements.** No information.**Status and Conservation.** Not globally threatened. Restricted-range species: present in Caripé-Paria Region EBA, Cordillera de la Costa Central EBA and Santa Marta Mountains EBA. Common in Colombia; in Venezuela, frequently recorded in Henri Pittier National Park.**Bibliography.** Flieg (1998), Hilty & Brown (1986), Meyer de Schauensee (1949, 1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Phelps & Phelps (1958), Snyder (1966), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Todd (1943), Visbal *et al.* (1996), Wetmore (1939).

## 38. Crested Quetzal

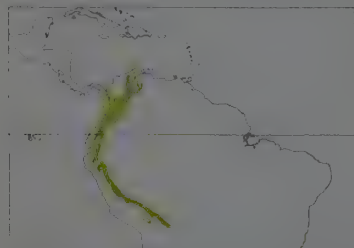
*Pharomachrus antisianus*

French: Quetzal antisien

German: Kammtrogon

Spanish: Quetzal Crestado

Other common names: Crested Trogon

**Taxonomy.** *Trogon Antisianus* d'Orbigny, 1837, Yungas, Bolivia.Forms a superspecies with *P. mocinno*, with which has sometimes been considered conspecific; *P. fulgidus* may belong to same superspecies. Monotypic.**Distribution.** N Colombia and NW Venezuela S along Andes to Ecuador, Peru and WC Bolivia.**Descriptive notes.** 33-34 cm. Male with orange-yellow bill, metallic green head with short forehead crest, unique in genus, iris red; plumage metallic emerald-green, with lower breast to undertail-coverts red; elongate wing-coverts and upptail-coverts, latter extending c. 2.5 cm beyond tail; outer 3 rectrices white, and when folded, undertail appears mostly white. Differs from similar *P. mocinno* in crest not being filamentous, so head more "conventional" in appearance (although base of bill covered by feathers), and lacks extended tail-streamers. Female with bill blackish to yellow, head greyish-brown withvirtually no crest, breast brownish, undertail dark with outer 3 rectrices barred whitish on outer webs and tips; almost identical to female *P. mocinno*, but tail shorter and head duller. Immature with pale webs on outer secondaries. Voice. Song apparently undocumented, but probably very similar to that of *P. mocinno*; call a loud, deliberate "way-way-wayó", alarm a loud inflected "ka-ka-ka-ka" (variable number of notes).**Habitat.** Middle levels to subcanopy of humid upper tropical and subtropical forest, cloudforest, edge, and occasionally tall second-growth woodland; 1400-2800 m (lower seasonally) in Colombia, 1200-3000 m in Venezuela. Often alongside *P. auriceps*, but occurs in greatest abundance slightly lower down than latter.**Food and Feeding.** Fruits and berries, but also insects, lizards, frogs. Most often seen in trees with larger fruit such as *Persea* and *Ocotea*, notably *O. calophylla*; also takes *Ficus*, especially *F. cundinamarensis*.**Breeding.** Birds in breeding condition in Feb-Jun. Nest in hole in dead tree or limb. No further details known.**Movements.** In Colombia, downslope displacement to c. 1000 m appears to occur on Pacific slope in Jun-Aug.**Status and Conservation.** Not globally threatened. Reckoned to be fairly common generally in much of range. However, rather uncommon in Colombia, where present in Cueva de los Guácharos National Park and rare in Munchique National Park. In Ecuador present in Podocarpus National Park. In Peru, rare to uncommon in parts of N above 1000 m, and generally uncommon.**Bibliography.** Allen (1998), Butler (1979), Davis, T.J. (1986), Fjeldså & Krabbe (1990), Hilty (1985, 1997), Hilty & Brown (1986), Hornbuckle (1999), Meyer de Schauensee (1949, 1982), Meyer de Schauensee & Phelps (1978), Olrog (1968), Parker *et al.* (1982), Phelps & Phelps (1958), Rasmussen *et al.* (1994), Remsen & Taylor (1989), Ridgely & Gaulin (1980), Stotz *et al.* (1996), Wetmore (1968), Zimmer (1948).

## 39. Resplendent Quetzal

*Pharomachrus mocinno*

French: Quetzal resplendissant

German: Quetzal

Spanish: Quetzal Guatemalteco

Other common names: Quetzal, Northern/Magnificent Quetzal

**Taxonomy.** *Pharomachrus Mocinno* de la Llave, 1832, Guatemala and Chiapas.Forms a superspecies with *P. antisianus*, with which has sometimes been considered conspecific; *P. fulgidus* may belong to this superspecies. Synonyms of *mocinno* include *paradisus* and *resplendens*. Species name sometimes misspelt *mocono*. Two subspecies recognized.**Subspecies and Distribution.***P. m. mocinno* de la Llave, 1832 - S Mexico (Oaxaca and Chiapas), Guatemala, Honduras, E El Salvador and NC Nicaragua.*P. m. costaricensis* Cabanis, 1869 - Costa Rica (except Cordillera de Guanacaste) and W highlands of Panama (E, at least formerly, to Veraguas).**Descriptive notes.** 36-40 cm, with tail-streamers up to 65 cm more; 180-210 g. Male nominate race with bill yellow, partly hidden by green filamentous feathers radiating in laterally compressed circle from around eye, giving head a bristling, short-crested appearance; upperparts, throat and upper breast bright iridescent green (shifting to blue at some angles), including elongate greater coverts (extending beyond line of closed wing) and 4 narrow, flexible, filamentous upptail-coverts ("streamers"); flight-feathers blackish; mid-breast to undertail-coverts red; undertail white. Female with variably blackish to yellow bill, bronze-green head, green upperparts, throat and upper breast, fairly elongate greater coverts and upptail-coverts, buff outer webs of primaries; mid-breast to mid-belly grey, then red to undertail-coverts; upptail blackish, undertail broadly barred greyish-black and white. Immature male like female, but bill yellow, bronzier above, undertail with more white. Race *costaricensis* slightly smaller, with shorter, narrower tail plumes. Voice. Song a steady "k'yoi-k'yow, k'yoi-k'yow, k'yoi-k'yow, k'yoi-k'yow"; calls include hard "kwah", steady "ka-ka-ka...", and in display-flight or agitation a rolling chatter, "perwicka" or "waka-waka-waka!".**Habitat.** Canopy and subcanopy (sometimes much lower) of undisturbed humid epiphyte-laden evergreen montane forest, cloudforest, thickly vegetated ravines and cliffs, edge, park-like clearings and pastures, and open situations with scattered trees adjacent to forest; 900-2275 m in Oaxaca, Mexico, but from 1200-1500 m up to 3200 m farther S.**Food and Feeding.** Fruit; also insects, small frogs, lizards and snails. Largely frugivorous, strongly preferring fruits of Lauraceae. Thus, foods recorded at Monteverde, in Costa Rica, include 18 species of Lauraceae (5 *Ocotea*, 4 *Nectandra*, 2 *Phoebe*, along with *Beilschmiedia* and *Persea*), as well as *Gualteria* (2 species), *Ficus* (2 species), *Symplocarpon*, *Hampea*, *Hasseltia*, *Pouteria*, *Symplocos* (several species), *Artisia*, *Rubus*, *Eugenia*, *Conostegia*, *Mappia*, *Dendropanax*, *Citharexylum* (2 species), *Chione*, *Coussarea* and *Anthurium*. Of these, only 8 identified as being brought to young, with only 2 lauraceous plants (*Ocotea tonduzii* and *Nectandra salicina*), although latter made up 80% of total fruit items; animal items brought to same nest totalled 121 invertebrates, of which 52 were beetles and their larvae (including Scarabaeidae), 35 orthopterans (chiefly Tettigoniidae) and 26 moth larvae (including Sphingidae), these 3 groups making up 97.5% of all insects delivered, also 9 lizards (all *Norops*) and 8 snails. Young fed almost exclusively insects in first 10 days. Sallies to pluck fruit or snatch animal prey from trees.**Breeding.** Mar-Apr in Mexico, although a report from Chiapas of May-Jul/Aug; May-Jun in El Salvador, Mar-May in Guatemala, Mar-Jun (often 2 broods) in Costa Rica. Territory in Guatemala 6-10 ha. Nest a deep, unlined cavity with single entrance, 4-3-27 m up in decaying trunk or stump in forest or nearby clearing; of 10 nests in Guatemala, mean height of stub 12.4 m and of nest 9.4 m, with most favoured tree *Brosimum costaricanum*. Eggs 1-2; incubation 17-19 days; nestling period 23-31 days. Reported that 80% of chicks die before fledging and, of those that fledge, another 80% die before adulthood.**Movements.** Resident in Mexico, but altitudinal shifts, presumably in response to changes in fruit abundance; telemetry work at El Triunfo Biosphere Reserve showed seasonal use of coffee-plantation buffer zones at lower elevations in non-breeding period. Recolonization, after 25 years' absence, of a forest patch in Chiapas indicates dispersive capacity. Telemetry studies in Costa Rica showed complex local migrations linking 4 montane life zones: after Jul in one year birds moved down Pacific slope to patches at 1300-1450 m, and in next year to patches at 1100-1350 m, in both years remaining until Oct/Nov, thereafter moving across continental divide to pre-montane Atlantic slope rainforest at 700-1200 m, remaining there until Jan, when they returned to breeding grounds.**Status and Conservation.** Not globally threatened. CITES I. Currently considered Near-threatened. Considered Vulnerable in 1970's, but subsequent evidence suggested that it was reasonably secure; new knowledge of local migratory behaviour strongly indicates need for status review. Fairly common to common where habitat untouched, but uncommon to rare in much of range owing to forest clearance and hunting for plumes. Threats include habitat clearance, felling of "honey-trees", poaching, lack of law enforcement, indigenous exploitation of forest resources. In Mexico still fairly widespread, surviving apparently wherever as little as 8 km<sup>2</sup> of cloudforest persists, but seriously at risk in N Chiapas through habitat loss and hunting; uncommon in El Triunfo Biosphere Reserve; in 1930's became isolated in NW Chiapas through spread of cultivation (especially coffee), leaving population there of c. 1000-2000 individuals. In Guatemala, also suffered greatly from clearance of forest for coffee plantations in 1880-1930, and from plume-hunting, but still fairly common in 1960's; now the national bird, and is present in Sierra de las Minas Biosphere Reserve, which, with 236,000 ha, is probably largest contiguous protected cloudforest in Central America. In El Salvador, prediction of extinction by mid-20th century through deforestation was not fulfilled, but by 1970's probably only the tiny Montecristo area sustained a viable small population. In Honduras locally fairly common, having suffered less persecution than farther N; very common 1930-1950 in Montaña de Pijol, in Yoro; in 1970 country was thought to hold largest population N of Costa Rica; a few survive in La Tigra National Park. No data for Nicaragua since reported as locally distributed in few remaining areas of cloudforest in 1970. In Costa Rica, species has proved resilient: in 19th century, plume trade caused it to be hunted to near-extinction in all accessible areas, but evidently recovered, since capture for pet trade was rife in 1950's and 1960's (100 pairs annually exported to zoos and collectors, 1956-1966), continuing into 1970's; remains fairly common, however, persisting in largely deforested areas if remnant woods contain good feeding and nesting trees, with large



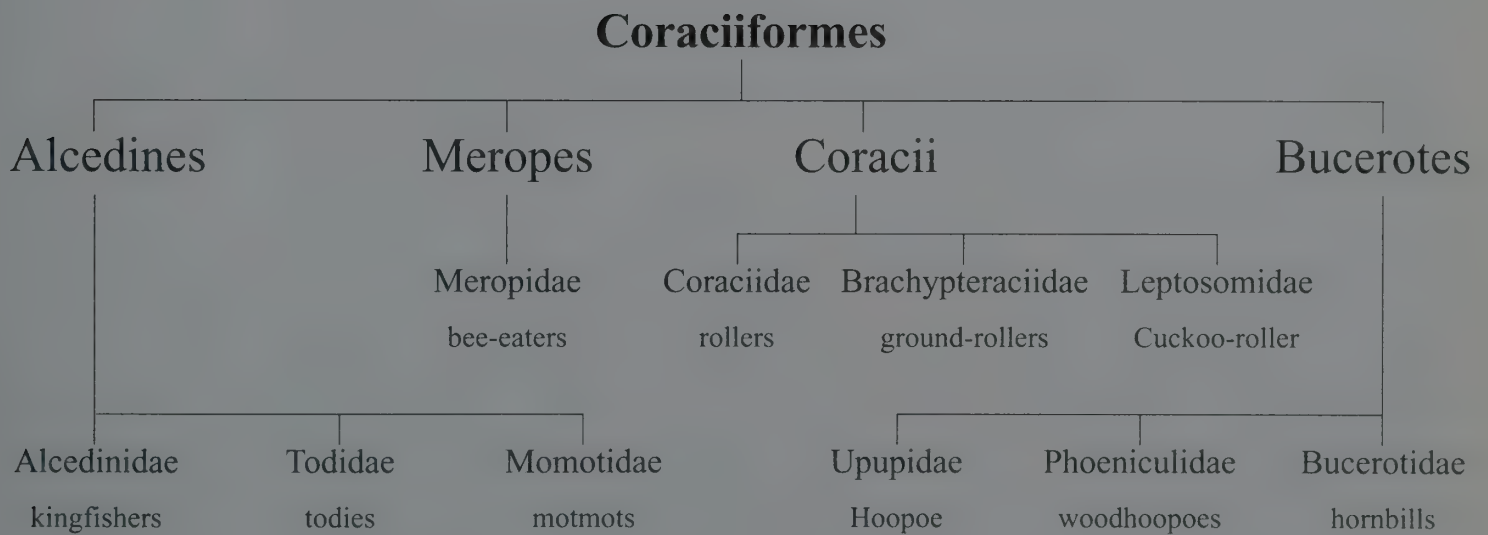
stable population in most mountainous areas, not in immediate danger, and present in Volcán Poás, Braulio Carrillo and Chirripó National Parks, also in Monteverde Forest Preserve, although the c.50 pairs in latter need supplementary protection of steadily diminishing forest patches up to 5 km outside and 600 m downslope. In Costa Rica, extrapolation based on density extremes of 2.7-2.9 birds/km<sup>2</sup> gave population estimates of 12,868-13,821 in Talamanca forest in 1977 and 4652-4997 in largest protected area (La Amistad National Park); given that 185 km<sup>2</sup> would hold c. 500 individuals, in early 1980's there were 3 large forested areas and 9 protected areas in Costa Rica which could support such "genetically viable" populations; however, elevational movements demonstrate necessity of establishing corridors between higher and lower forest areas. Uncommon to fairly common in Panama, where numbers continue to decline, owing mostly to forest clearance, but some persecution suspected; no longer found lower than 1500 m; c.100 estimated to survive in early 1970's around Volcán Barú, where a century earlier the species had been abundant (area now infiltrated by road-cutting potato farmers).

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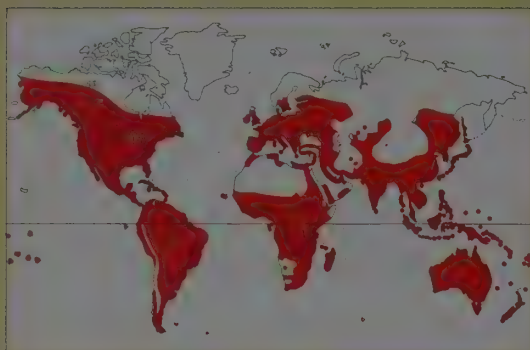




# Order CORACIIFORMES



Class AVES  
Order CORACIIFORMES  
Suborder ALCEDINES  
**Family ALCEDINIDAE (KINGFISHERS)**



- Small to medium-sized, compact birds with long, straight and dagger-like bill, short legs and often with bright plumage colours.
- 10-46 cm.



- Cosmopolitan.
- Mostly forest or woodland, often by water, some in open woodland away from water, one in desert scrub.
- 17 genera, 92 species, 315 taxa.
- 11 species threatened; 2 subspecies extinct since 1600.

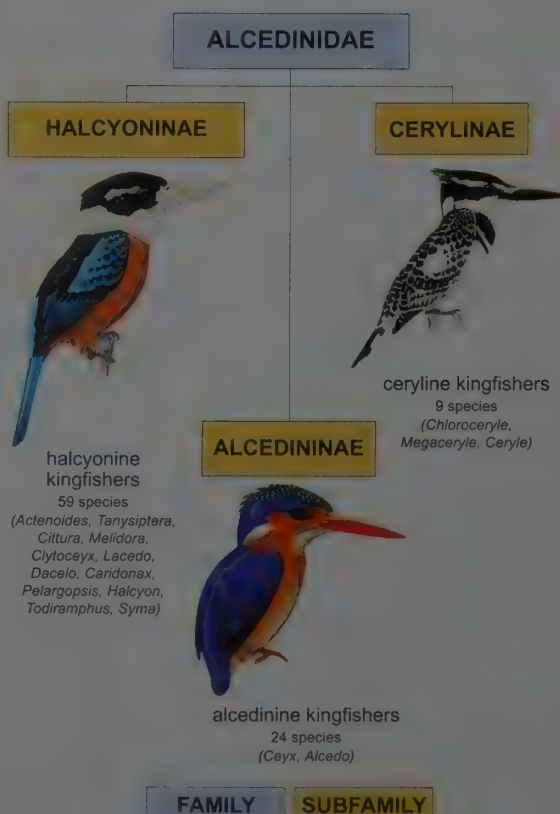
### Systematics

The fossil record of the kingfishers is poor, and there are few examples from earlier than the Quaternary. Fossil evidence exists to suggest that coraciiform birds were the dominant arboreal perching birds in North America and Europe by the early Tertiary, 60 million years before present. Some that were previously thought to be kingfishers have now, however, been reclassified. *Halcyornis* from the Lower Eocene of Kent, in England, has been variously considered to be a gull (Laridae) or a kingfisher, but is now thought to be the sole representative of an extinct family, the Halcyornithidae, perhaps closest to the rollers (Coraciidae) and the cuckoo-rollers (Leptosomidae), in the Coraciiformes. Similarly, fossils of *Protornis* from Switzerland, formerly considered to be kingfishers, have subsequently been allocated to the motmots (Momotidae). Nevertheless, fossil kingfishers have been found in the Lower Eocene of Wyoming, the Middle Eocene of Germany and the Eo-oligocene of France, about 30-40 million years ago, and from the Miocene of Australia, 5-25 million years ago.

Around the world, several kingfishers have been reported from the Quaternary Period, up to 1 million years ago, which cannot be distinguished from living species. These include the Laughing Kookaburra (*Dacelo novaeguineae*) and the Red-backed (*Todiramphus pyrrhopygus*) and Azure Kingfishers (*Alcedo azurea*), from deposits in Australia, the Sacred Kingfisher (*Todiramphus sanctus*), from Australia and New Caledonia, and the Giant Kingfisher (*Megaceryle maxima*) and White-throated Kingfisher (*Halcyon smyrnensis*), from Israel. Similarly, the Belted Kingfisher (*Megaceryle alcyon*) has been identified from several deposits in North America, the Amazon Kingfisher (*Chloroceryle amazona*) from Brazil, and the Common Kingfisher (*Alcedo atthis*) from deposits in England and elsewhere in Europe. A new, undescribed fossil species of *Ceryle* has recently been found in Florida, USA, dated at 2 million years ago.

Several criteria can be used to determine the likelihood of one group of kingfishers being of more recent origin than another. A generalized diet and a non-specialized feeding technique are likely to have preceded more specialized ones, so that catching insects in flight or diving into water for fish are probably adaptations from a more generalized "sit-and-wait" technique of catching insects and other small animals on the ground. An old, stable habitat, such as rainforest, is more likely to have ancestral

forms, while it is probable that species in previously glaciated regions are recent invaders. Ancestral species are likely to be distinctive forms, in small genera and without close relatives, while recent, rapidly evolving taxa will have many, closely related species or subspecies. Using these criteria, the oldest, ancestral forms of the family are to be found mainly in the rainforest of Malesia, encompassing the regions of Indochina, Indonesia, Malaysia and New Guinea. They are primarily members of the subfamily Halcyoninae, but include some species of *Ceyx* in the Alcedininae.



Subdivision of the  
*Alcedinidae*

[Figure: Tim Worfolk &  
Norman Arlott]



A typical halcyonine kingfisher, the Mangrove Kingfisher is one of eleven species that make up the genus *Halcyon*. These all appear to be closely related, having similar habits, territorial displays and songs, and distinctive wing patterns. Several other genera, however, seem to have much in common with the typical *Halcyon* species, and have sometimes been merged with *Halcyon*, thereby creating a large genus of 36 or even 40 and more species.

[*Halcyon senegaloides*, Wavecrest, eastern Cape Province, South Africa. Photo: Geoff McIlleron]



Traditionally, the kingfishers have been grouped in a single family, the Alcedinidae, within which apparently closely related genera have been arranged to form three separate subfamilies. The results of relatively recent DNA-DNA hybridization studies, however, appear to indicate that there are wide gaps between these three groups of kingfishers, to the extent that some authors prefer to accord each of them family status, as the Alcedinidae, the Halcyonidae and the Cerylidae. At the molecular-genetic level, the last two of those seem to be more closely related to one

another than either is to the Alcedinidae, which is considered to be the ancestral group.

Modern taxonomists, using molecular-genetics, have grouped the kingfishers with the bee-eaters (Meropidae), the todies (Todiidae) and the motmots in the same suborder. Recent traditional classifications, however, usually divide this assemblage of families into two suborders, the Alcedines, which includes kingfishers, todies and motmots, and the Meropes, for the bee-eaters. In addition, as already mentioned, the three separate taxonomic groups of kingfishers are generally treated as subfamilies within the family Alcedinidae: namely, the Halcyoninae, the Alcedininae and the Cerylinae. Furthermore, morphological and behavioural data suggest that the cerylinae are closer to the alcedinines than they are to the halcyonines, and that the halcyonines are the ancestral group from which the others evolved. This discrepancy with the findings of DNA studies might be caused by some of the small alcedinine kingfishers having much quicker generation turnovers than do the larger halcyonines and cerylinae, so that the latter may be older than the DNA evidence indicates.

The main divisions among the kingfishers are, therefore, well known and widely accepted. The major problem is in deciding at which level these differences should be recognized. Apart from the difficulties over whether the three subfamilies merit elevation to family rank, there are also problems at the genus level. For example, the Halcyoninae have been divided by various authors into 15, twelve and eight genera. In addition, it is not easy to determine whether certain island populations of kingfishers should be treated as subspecies or as full species.

Of the three subfamilies, the Halcyoninae is by far the largest and the most diverse, containing 59 species. It includes some genera that are likely to be near the ancestors of the family and others that are extremely specialized, while some of its members show evidence of recent radiation and incipient speciation. There are six species in the genus *Actenoides*. Three of these, the Blue-capped (*Actenoides hombroni*), the Spotted (*Actenoides lindsayi*) and the Rufous-collared Kingfishers (*Actenoides concretus*), are sometimes treated as conspecific, although they seem sufficiently distinct to be treated as full species which, together, form a

Even the rather distinctive genus *Actenoides* has, at times, been included in *Halcyon*, although there would seem to be good reasons for separating it. A good case for this can be provided by the Rufous-collared Kingfisher, the male of which, shown here, has a dark blue back and wings, whereas the female has these parts of the plumage dark green with prominent yellowish spots. Sexual plumage dimorphism is, in fact, a characteristic feature of all six *Actenoides* kingfishers, being best demonstrated by this species, whereas the members of the genus *Halcyon* show either little difference between the sexes or none at all.

[*Actenoides concretus borneanus*, Bentuang-Karimun National Park, western Kalimantan, Borneo. Photo: Doug Wechsler/VIREO]





The little Madagascar Kingfisher is closely related to the Malachite Kingfisher (*Alcedo cristata*) of the African mainland, with which it forms a superspecies. The two are very similar in appearance and might be thought to be conspecific, but the Madagascar species has a somewhat different feather pattern on the crown and a blackish bill, the latter being red in the Malachite Kingfisher. Both appear to have close affinities also with the red-billed White-bellied Kingfisher (*Alcedo leucogaster*) of western and central Africa, all three differing from other *Alcedo* in including some terrestrial insects in their diet. Some taxonomists prefer to emphasize this difference by combining the three in a separate genus *Corythornis*.

[*Alcedo vintsioides*  
*vintsioides*,  
Mantadia National Park,  
Madagascar.  
Photo: Nick Garbutt]

superspecies. All species in this genus show some degree of sexual dimorphism, this being most pronounced in the Rufous-collared Kingfisher, the male of which has a dark blue back and wings, the female having a dark green back and wings with yellowish spots. The Moustached Kingfisher (*Actenoides bougainvillei*) of Bougainville and Guadalcanal, in the Solomon Islands, shows greater differences from the other *Actenoides* in terms of both plumage and distribution, which may reflect a more distant rela-

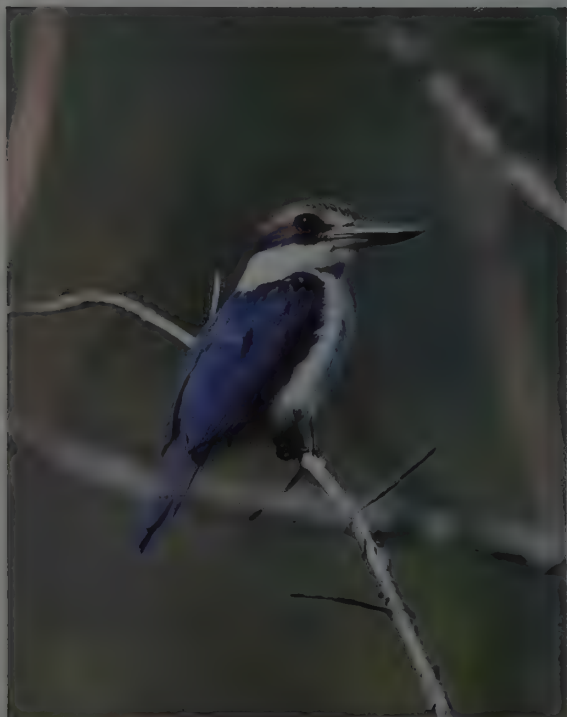
tionship. Its plumage does, however, exhibit certain similarities to that of some species of paradise-kingfisher, particularly the Brown-headed (*Tanysiptera danae*) and Buff-breasted Paradise-kingfishers (*Tanysiptera sylvia*), and it may provide a link between these two genera.

The eight species of paradise-kingfisher represent the clearly defined genus *Tanysiptera*, all members of which have long central tail-streamers in the adult. Some species are very sedentary, and this has led to the differentiation of isolated populations, particularly those on islands. This is clearly evident in the Common Paradise-kingfisher (*Tanysiptera galatea*), which has numerous subspecies in a range extending from Sulawesi to New Guinea. The Kofiau Paradise-kingfisher (*Tanysiptera ellioti*) and the Biak Paradise-kingfisher (*Tanysiptera riedelii*) are also sometimes treated as subspecies of the Common Paradise-kingfisher, but their distinctive plumage differences and geographical separation suggest that both should be treated as full species. Apart from being smaller, the Aru Paradise-kingfisher (*Tanysiptera hydrocharis*) is very similar to the Common Paradise-kingfisher. It, too, could be considered a subspecies of the latter were it not for the fact that the two co-exist in the Fly River region of southern New Guinea, which the Aru species probably invaded after having diverged on the nearby islands of that name.

Within the subfamily Halcyoninae are several monotypic genera. The Lilac-cheeked Kingfisher (*Cittura cyanotis*) is the sole member of its genus and has no close relatives, although it does show some slight similarities to the *Tanysiptera* species, especially the Brown-headed Paradise-kingfisher. Similarly, the Hook-billed Kingfisher (*Melidora macrorrhina*) is highly distinctive, with the unusual habits of being nocturnal and apparently digging in the leaf litter for its food. Its plumage exhibits a close resemblance to that of the juvenile Common Paradise-kingfisher, and it shares similar calls and alarm calls with that species, indicating that the two may be related. Its brown plumage and its hooked bill also suggest a possible link with the kookaburras in the genus *Dacelo*. The unique Shovel-billed Kingfisher (*Clytoceyx rex*), again the only species in its genus, has an extraordinary bill, specialized for digging in the forest floor, but

The taxonomic problems of the Alcedinidae are well demonstrated by the case of the Collared Kingfisher. Ranging as some 50 races from north-east Africa and south Asia to Australia and the south-central Pacific, its taxonomy represents a veritable nightmare. While there seems little doubt that it is closely related to the Sacred and Chattering Kingfishers (*Todiramphus sanctus* and *T. tutus*), the boundaries between the three species in the Pacific are far from clear. For example, some of the populations assigned to the Collared Kingfisher, including the Tongan one, shown here, could equally be treated as races of the Chattering Kingfisher.

[*Todiramphus chloris sacer*,  
'Eua, Tonga,  
South Pacific.  
Photo: C. & D. Frith]





certain aspects of its plumage, such as the blue tail and rump of the male and the rufous tail of the female, demonstrate a possible relationship with the kookaburras.

Although sometimes placed in the genus *Halcyon*, the White-rumped Kingfisher (*Caridonax fulgidus*) shows no clear affinities with any of those species and is considered best placed in a monotypic genus. It is a striking blue-and-white bird, showing some plumage similarities with the Moustached Kingfisher. Its call is not unlike those of some *Dacelo* kookaburras, which also share with it the habit of cocking the tail when calling.

Of the four kookaburras, the forest-dwelling Rufous-bellied Kookaburra (*Dacelo gaudichaud*) seems likely to be nearest to the ancestral form, with the other species radiating into more open, savanna-type habitats. The Spangled Kookaburra (*Dacelo tyro*) may have differentiated in the Aru Islands and subsequently reinvaded mainland New Guinea, a similar situation to that of the Aru Paradise-kingfisher. The Blue-winged Kookaburra (*Dacelo leachii*), or an ancestral form of it, apparently crossed the Torres Strait to spread through the northern savannas of Australia, and an offshoot gave rise to the Laughing Kookaburra, which has spread much farther south, into temperate woodland. It is of interest here to note that, although the Laughing Kookaburra was for many years known as *Dacelo gigas*, its correct scientific name, by the rules of priority, is *Dacelo novaeguineae*, even though the species does not occur in New Guinea, from where Sonnerat's first description of it seems to have been a deliberate falsification. The Banded Kingfisher (*Lacedo pulchella*) of South-east Asia and the Greater Sundas may be an early offshoot of the kookaburras. Although it is geographically separated from them, and placed in its own genus, the sexual dimorphism of its plumage, the upperparts being blue in the male and rufous in the female, reveals affinities with the kookaburras.

All of the remaining 36 species of halcyonine kingfishers share many similarities, and show little more in the way of plumage variation than do, for example, the four *Dacelo* kookaburras. For this reason, they are sometimes all placed in the genus *Halcyon*. Such an arrangement, however, creates a very large, unwieldy genus which obscures some of the clear natural groups

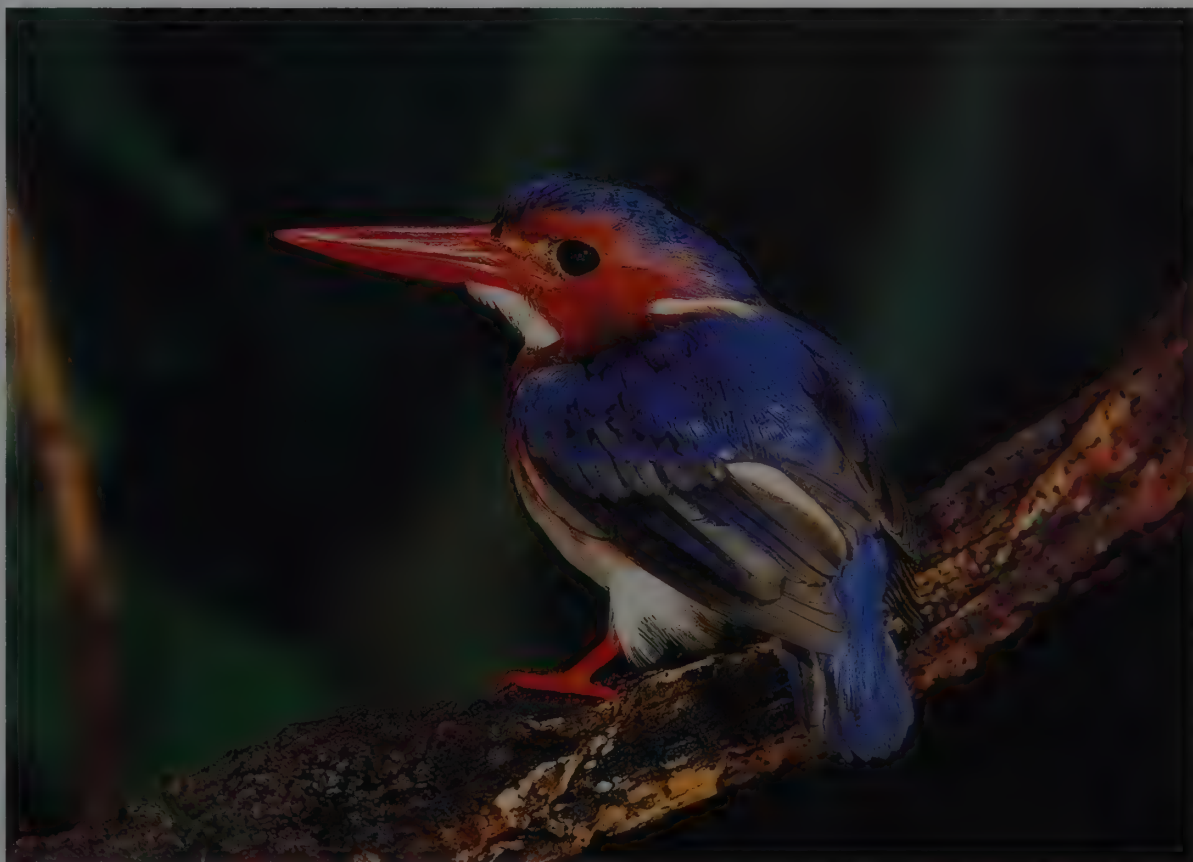


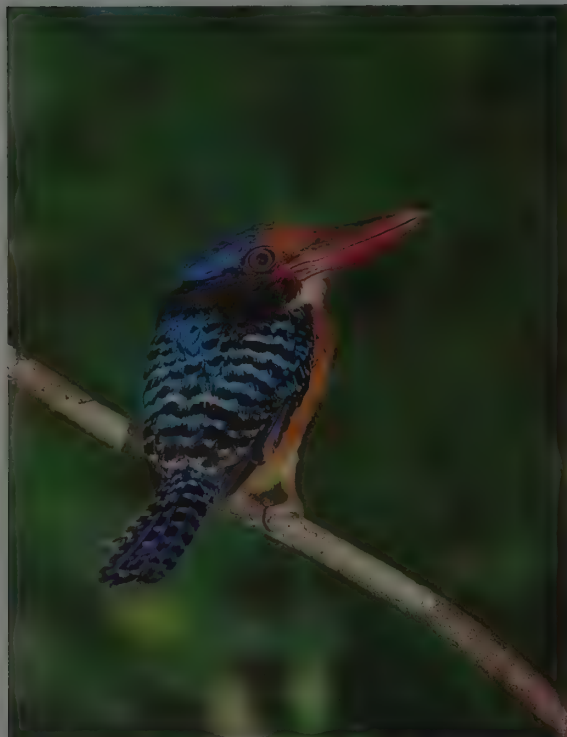
among its species. It is considered better, therefore, to split this assemblage into four genera, while recognizing that the differences between them are not great.

Three large kingfishers are thus combined in the genus *Pelargopsis*. These are the Stork-billed (*Pelargopsis capensis*), the Black-billed (*Pelargopsis melanorhyncha*) and the Brown-

A characteristic of most alcedinids, including the White-bellied Kingfisher, is their brilliant plumage colours. There is a popular misconception that these colours are produced by iridescence, dependent on the angle of the light, but they are, in fact, caused by details of the feather structure that influence the light's rays. Minute air-filled cavities within the keratin of the feather barbs act as a cloudy medium, scattering short wavelengths of white light to produce blue colours; underlying the cloudy medium, a layer of melanin absorbs longer wavelengths to give reds. Tiny granules in the outer barb layers act as a filter: reddish-brown granules produce violet and purple colours, or the distinctive chestnut shown by many species, and yellow ones produce green.

[*Alcedo leucogaster leucogaster*, above Etome, Cameroon. Photo: Doug Wechsler/VIREO]





winged Kingfishers (*Pelargopsis amauroptera*), characterized by their large size and long, heavy bill, which is probably associated with the diet of crabs and fish. The Mountain Kingfisher (*Syma megarhyncha*) and the Yellow-billed Kingfisher (*Syma torotoro*) of New Guinea and northern Australia have a distinctive plumage, with a rufous head with black patches around the eyes and on the nape and/or crown. In addition, the cutting edges

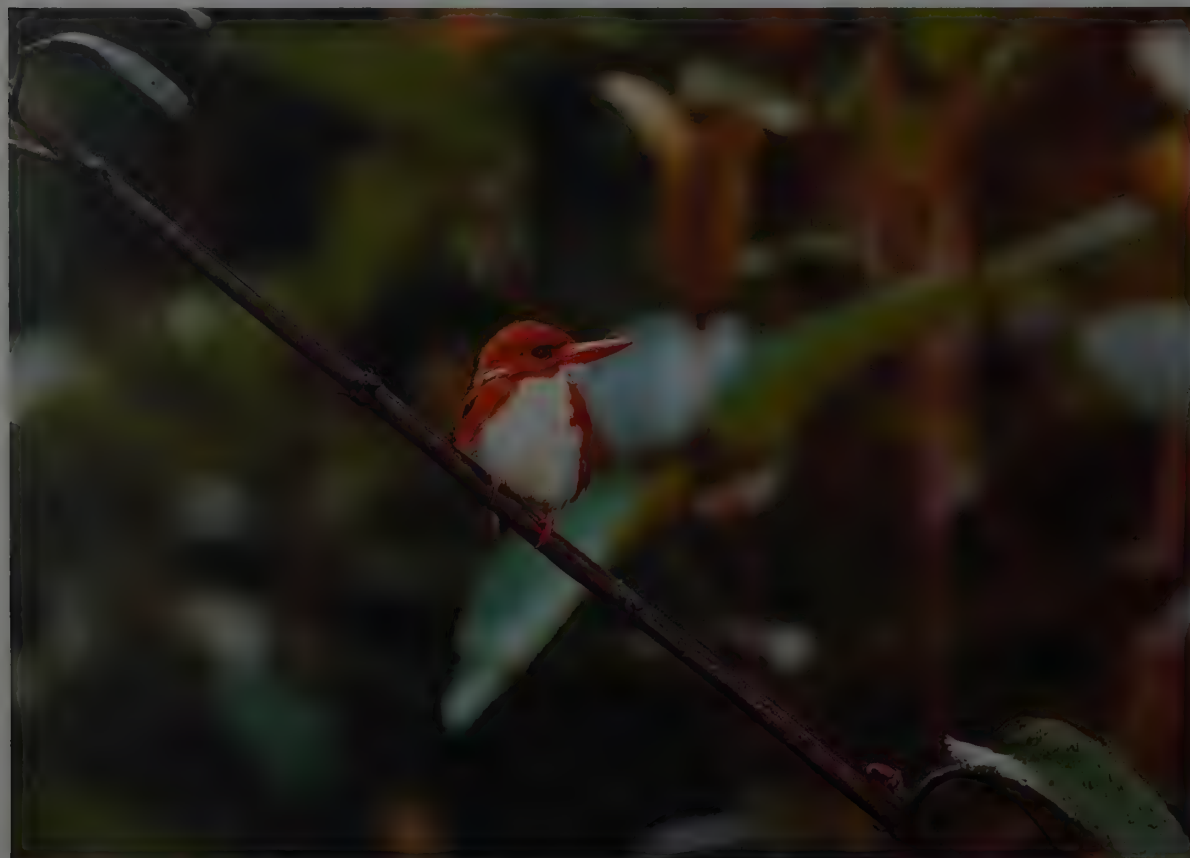
of the bill also have unusual serrations, the function of which is, however, unknown.

Although generally placed in the genus *Halcyon*, the Ruddy Kingfisher (*Halcyon coromanda*) shows few similarities with other members of that genus and is sometimes assigned to a monospecific genus *Entomothera*. It bears some morphological resemblance to the much larger Brown-winged Kingfisher. Otherwise, three further species from Asia and seven from Africa are combined in *Halcyon*. These ten are evidently closely related, with distinctive wing patterns, and similar habits, territorial displays and songs. The White-throated Kingfisher and the Javan Kingfisher (*Halcyon cyanoventris*) are closely related and form a superspecies, while the Chocolate-backed Kingfisher (*Halcyon badia*) of African rainforest shows strong affinities with them. The Black-capped Kingfisher (*Halcyon pileata*) of Asia and the Grey-headed Kingfisher (*Halcyon leucocephala*) of Africa are also considered to constitute a superspecies, having affinities with the Afrotropical Brown-hooded (*Halcyon albiventris*) and Striped Kingfishers (*Halcyon chelicuti*). Interestingly, several plumage similarities exist between the Striped Kingfisher and the Red-backed Kingfisher of Australia, suggesting that the Striped Kingfisher may have originated from the *Todiramphus* group of kingfishers. On the other hand, differences in territorial behaviour and in feather proteins indicate that it is more closely related to the other African *Halcyon* species. The remaining three Afrotropical species, the Woodland (*Halcyon senegalensis*), the Mangrove (*Halcyon senegaloides*) and the Blue-breasted Kingfishers (*Halcyon malimbica*), are closely related to one another, the first two forming a superspecies.

The genus *Todiramphus*, sometimes relegated to a subgenus of *Halcyon*, contains a total of 20 species. These are found mainly in Malesia, Australia and the Pacific, with the Collared Kingfisher (*Todiramphus chloris*) extending westwards to Africa. It is worth noting that Lesson, when he first named the genus, in 1827, spelt it incorrectly; under the international rules of nomenclature, however, this earlier version should stand, rather than the commonly used corrected name "*Todirhamphus*". These species use a range of habitats, forest, woodland and sea-shore but

Most kingfishers have a long, straight, dagger-like bill, generally red or black in colour. In species which capture prey on the ground, such as the Banded Kingfisher, the bill is relatively shorter and quite broad. Typically, the legs are short, and the feet of most species have four toes, three pointing forward and one back. The strikingly barred upperparts of the Banded Kingfisher, blue and black in the male and rufous and black in the female, immediately separate it from all other alcedinids. It is also interesting to note that, in Borneo, this species is considered to be a bird of favourable omen.

[*Lacedo pulchella melanops*, Mendolong.  
Photo: Doug Wechsler/VIREO]



Although kingfishers in general are small to medium-sized birds, there is a wide variation in size among the members of this family. The smallest of all are the aptly named dwarf-kingfishers and pygmy-kingfishers in the genus *Ceyx*. The tiny Madagascar Pygmy-kingfisher, for example, is only 13 cm long and weighs no more than about 20 g. This is one of two closely related genera that make up the subfamily Alcedininae. The seven *Ceyx* species have a vertically flattened bill, and are primarily insectivorous forest-dwellers; three of them, and one form of a fourth, have rufous or chestnut upperparts. The *Alcedo* species, blue above and with a laterally flattened bill, feed chiefly on fish and aquatic insects.

[*Ceyx madagascariensis madagascariensis*, Mantadia National Park, Madagascar.  
Photo: Nick Garbutt]



A unique characteristic of the Hook-billed Kingfisher, shown well by this captive individual, is the distinctive hooked tip of the upper mandible, this being the principal reason for the species' placement in a monotypic genus. This kingfisher is thought to dig for food among leaf litter, which would explain the hooked bill, and it differs further from other alcedinids in its largely nocturnal habits. At 27 cm in length and weighing about 100 g, this species is by no means the biggest of the family, but it does help to illustrate the size range found among the Alcedinidae.

[*Melidora macrorrhina*.  
Photo: C. H. Greenewalt/  
VIREO]

share a suite of plumage characters that are common to most of them. They generally have white or buffy underparts and the back, wings and tail are dark blue to pale green. Their bill is black with a horn-coloured base to the lower mandible and they have a dark line through the eye and ear-coverts to divide the dark crown from a pale collar, and a white or buffy loreal spot.

A group of eight blue-and-white kingfishers is found from the Philippines, through Indonesia, New Guinea and Australia, to Vanuatu. Six of these are closely related, and form a superspecies. These are the Blue-and-white (*Todiramphus diops*), the Lazuli (*Todiramphus lazuli*), the Forest (*Todiramphus macleayii*), the New Britain (*Todiramphus albonotatus*), the Ultramarine (*Todiramphus leucopygius*) and the Chestnut-bellied Kingfishers (*Todiramphus farquhari*). The males generally have white underparts, collars or backs and the females have more blue in these areas, although the Chestnut-bellied Kingfisher is an exception to this. The larger Blue-black (*Todiramphus nigrocyaneus*) and Rufous-lored Kingfishers (*Todiramphus winchelli*) are clearly related to this group, but show a different kind of sexual dimorphism.

The Chestnut-bellied Kingfisher exhibits several similarities, including call, a flat bill and buffy underparts, with the remaining twelve *Todiramphus* species, which are basically green and white in colour. One of these, the Collared Kingfisher, has a huge distribution, extending from the Red Sea and the east coast of Africa westwards to the Samoan Islands, in the south-central Pacific. Over this range of approximately 16,000 km, the species has differentiated into 50 or so recognized subspecies, some of which, such as the white-headed race *albicilla* from the southern Mariana Islands, are quite distinctive, while others differ only in slight details of plumage coloration. Closely related to the Collared Kingfisher are the Micronesian Kingfisher (*Todiramphus cinnamominus*) and the Talaud Kingfisher (*Todiramphus enigma*). Both of those are found living and breeding alongside the Collared Kingfisher and so they must be reproductively isolated from it, but otherwise they are similar enough to be considered merely subspecies of it. A taxon which has become extinct in recent times is known from only a single specimen taken on Miyako-



jima in the southern Ryukyu Islands, between Japan and Taiwan; named *miyakoensis*, it is usually considered to have been a subspecies of the Micronesian Kingfisher, but some authors have suggested that it might perhaps have been a full species. Related to this group of three or four species are the Sombre Kingfisher (*Todiramphus funebris*) and the Beach Kingfisher (*Todiramphus saurophagus*). The latter has white-crowned and green-crowned

The Javan Kingfisher is a typical Halcyon, a genus of eleven mostly medium-sized African and Asian species which share similar behaviour and vocalizations. It shows the long, red bill, the rather thickset, dumpy build and the bright plumage colours, including a distinctive wing pattern, that are characteristic of all but one of the species of that genus. The sole exception is the Ruddy Kingfisher (*Halcyon coromanda*) of Asia, which, apart from its much smaller size, is in some respects closer in morphology to the Pelargopsis kingfishers.

[*Halcyon cyanoventris*,  
Java.  
Photo: Brian J. Coates/  
Lynx]



morphs, both of which can occur in the same brood of nestlings, but the percentages of each morph differ on different islands. The subspecies *matthei* of the Collared Kingfisher exhibits ■ similar variation in crown colour.

The Sacred Kingfisher is smaller than the Collared Kingfisher, and has more buffy underparts, but is similar in its behaviour and habitat preferences. It is distributed from Australia to the islands of Western Samoa. In the latter region, the subspecies *recurvirostris* is sometimes treated as a distinct species, but its cinnamon-buff collar, breast and belly and its flattened bill lie within the range of variation shown by the four other subspecies of the Sacred Kingfisher. Associated with the Sacred Kingfisher in ■ superspecies are five other halcyonines. The Cinnamon-banded Kingfisher (*Todiramphus australasia*) has cinnamon underparts, collar and eyestripe, as well as a cinnamon crown in the race *interpositus*; its differences from the Sacred Kingfisher thus parallel those between the Micronesian and Collared Kingfishers. The Chattering Kingfisher (*Todiramphus tutus*), widely distributed in Polynesia, has a flattened bill, suggesting that it is closer to the Sacred Kingfisher than it is to the Collared. One of its subspecies, *ruficollaris*, is the only kingfisher on Mangaia, in the Cook Islands, and is sometimes treated as ■ full species on account of the greater development of rufous on its eyebrow, hindcollar and breast; this, however, seems to represent merely the extreme of a range of plumage variation, and the taxon is probably better regarded as a race of the Chattering Kingfisher. The latter occurs together with the Tahiti Kingfisher (*Todiramphus veneratus*) on the island of that name, indicating that the two are reproductively isolated. The last two members of this superspecies, the Tuamotu Kingfisher (*Todiramphus gambieri*) and the Marquesas Kingfisher (*Todiramphus godeffroyi*), are normally treated as full species on the basis of their fairly distinctive plumage, but, being the only kingfishers on isolated islands, the validity of their specific status could be questioned.

There seems little doubt that the Collared, Sacred and Chattering Kingfishers are all closely related to one another, each with ■ range of subspecies isolated on islands, and the boundaries between the species are not at all clear in the Pacific. Some of the populations classified here as belonging to one of these

species could perhaps just as validly be assigned to another, while others that are treated as subspecies may well be full species. For example, the taxon *ruficollaris* on Mangaia Island, while considered to be a subspecies of the Chattering Kingfisher, could equally be a subspecies of the Sacred Kingfisher or, quite possibly, a separate species altogether. Similarly, the subspecies *marina*, *sacer*, *manuae* and *pealei* of the Collared Kingfisher may, in fact, be races of the Chattering Kingfisher. This rather unsatisfactory situation is unlikely to be resolved until detailed genetic research is undertaken, but this would not be easy given the scattered distribution of these populations over thousands of kilometres in the Pacific Ocean.

Even more problematic, however, is the business of determining the taxonomic status and relationships of the two kingfishers occurring in the Tuamotu Archipelago. Particular difficulties and uncertainties surround the position of the taxa *gertrudae*, confined to the island of Niau in the north, and *gambieri*, known only from Mangareva, over 2000 km to the south-east, in the Gambier group. The problem is made no easier by the fact that *gambieri* became extinct by about 1922, so its habits and behaviour remain a closed book. The complexities of the possible relationships of these forms have led to their being treated in a number of different ways by various authors. Bearing in mind the absence of sufficient data on the molecular genetics of these populations, there would appear to be three or four main approaches to the problem of *gambieri* and *gertrudae*. First, they could be seen as conspecific, forming a single species restricted to the Tuamotu Archipelago, an arrangement proposed by D. T. Holyoak and J. C. Thibault in 1977, and adopted by H. D. Pratt and colleagues in their 1987 guide to the birds of Hawaii and the tropical Pacific. An alternative view, and one preferred by C. H. Fry and others in their 1992 monograph, is to consider *gambieri* a subspecies of the more widespread Chattering Kingfisher, and to treat *gertrudae* as a separate monotypic species, the Niau Kingfisher, found only on the island of that name. A third possibility would be to raise both *gambieri* and *gertrudae* to two full, independent species, separate from the Chattering Kingfisher and from each other. Conversely, it might be argued by some that the most appropriate arrangement would



An unmistakable feature of the paradise-kingfishers is the remarkably elongated central tail feathers, up to 20 cm in length and protruding as thin streamers a long way beyond the rest of the tail. In the Buff-breasted Paradise-kingfisher, the only one of the eight species in which the streamers do not have a racquet at the tip, the male's central rectrices, as well as its other tail feathers, are significantly longer than those of the female. This difference in biometrics is unusual among kingfishers, which, with the exception of two of the Dacelo kookaburras, do not exhibit any notable sexual variation in measurements or weights.

[*Tanysiptera sylvia sylvia*, Mount Spec, near Townsville, Queensland, north-east Australia. Photo: C. & D. Frith]



Sexual plumage dimorphism among the kingfishers is limited. Where it does exist, it is normally manifested by a difference in colour in one part of the plumage, or the presence or absence of a patch of colour. The female Yellow-billed Kingfisher, for example, has a black crown patch, whereas the male's crown is entirely rufous. This species and its sole congener, the very similar Mountain Kingfisher (*Syma megarhyncha*), differ from all others in having a bright yellow bill.

[*Syma torotoro flavirostris*, Wesbit River, eastern Cape York, Queensland, north-east Australia. Photo: C. & D. Frith]



be to treat both taxa as subspecies of the Chattering, which otherwise occurs farther to the west, in the Society Islands and Cook Islands. On present information, however, neither of the last two treatments appears to have its champion amongst taxonomists. Although geographical distribution appears to have been one of the reasons behind the placing of *gambieri* as a subspecies of the Chattering Kingfisher, this seems difficult to justify. The two are separated by a greater distance than is *gambieri* from *gertrudae*, and in neither case are there any intervening populations of kingfishers. On the other hand, if plumage colour and pattern are deemed important, and if the form *ruficollaris*, occurring only on Mangaia in the Cook Islands, is indeed properly treated as a race of the Chattering Kingfisher, then one can argue that *gambieri* should likewise be placed with that species, as a subspecies intermediate in plumage between *ruficollaris* and the nominate race of the Society Islands. The Niau taxon, *gertrudae*, would then appear to be at an extreme, and perhaps sufficiently so to warrant separation as a species. The problem with this interpretation, however, is that the nominate form of the Chattering Kingfisher and the taxon *ruficollaris* are geographically very much closer to each other than either is to the supposedly intermediate *gambieri*. While *gertrudae* does, admittedly, appear rather different in plumage, this difference does not seem to be notably greater than is shown by many other alcedinid forms that are treated as subspecies rather than as full species. At the same time, a number of authorities do regard *ruficollaris* as a full species, presumably on the grounds of plumage characters and its geographical isolation from other forms of the Chattering Kingfisher.

In terms of appearance, the kingfishers of, respectively, Niau and the Gambier Islands may seem less similar to one another than does the latter to the Chattering Kingfisher and, especially, to *ruficollaris*. Nevertheless, they are the only two alcedinids known in the Tuamotu Archipelago, a fact which could be of some significance. It is conceivable that, in the past, some of the intervening islands in this south-central Pacific archipelago held populations of halcyonines that linked the two present forms together. Sea-level was much lower only about 12,000 years ago, and these islands would therefore have been considerably larger than they are today. Furthermore, one could even speculate that an eastward expansion took place of a species similar to the Sacred Kingfisher of Australia, one race of which today extends to Western Samoa. This could then have differentiated progressively into *tutus* and *veneratus*, then producing *gertrudae* and, finally, *godeffroyi*; this last form is widely recognized today as a separate species, the Marquesas Kingfisher. Under this scenario, the

current plumage differences between *gertrudae* and *gambieri* could be regarded as merely extremes of what was once a continuous variation through the Tuamotu Archipelago.

It has to be emphasized, of course, that all of these ideas are highly speculative and essentially subjective. For the time being, however, it seems best to regard the two Tuamotu taxa, *gertrudae* and *gambieri*, as conspecific, a course followed by conservationists at the beginning of the twenty-first century. In the meantime, a great deal of research is required, especially in the field of modern genetics, to enable a rational taxonomic review to be made of this intriguing group of Polynesian kingfishers.

The juvenile plumage is basically similar to that of the adults, though often a shade duller. In the genera *Halcyon* and *Todiramphus*, however, juveniles can often be identified by being mottled or faintly barred where the adults are uniform in colour. This ageing criterion can be seen in the Black-capped Kingfisher, a common species of south and south-east Asia. Adults of both sexes have a clean white collar, throat and breast, with the remaining underparts plain rufous. The somewhat less bright juvenile, on the other hand, as shown here, has a buff tinge to the white areas, and its breast has dusky or rufous scale-like markings; it differs further from its parents in having a small buff patch above the lores and a browner, less red, bill.

[*Halcyon pileata*, Mai Po, Hong Kong. Photo: Ray Tipper/Aquila]





Kingfishers have a swift and direct flight, with fast, regular whirring beats of the broad, short wings. They often pass by in a flash, before the observer has time to notice their presence, this being typical of the smaller species, which are also capable of making abrupt sharp-angled turns. Even the larger species, however, are fast fliers. Despite its huge size, 40 cm in length and weighing up to 330 g, the Ringed Kingfisher can move quickly through the air. This widespread inhabitant of waterbodies in Central and South America is a rather shy bird. If disturbed at its perch, it usually flies low over the water and out of sight, occasionally making a short detour over dry land between waters.

[*Megaceryle torquata torquata*, Pantanal of Brazil. Photo: Günter Ziesler]

Finally, the remaining member of this group of green-and-white *Todiramphus* species, the Red-backed Kingfisher, is clearly related to the Sacred Kingfisher group, but quite distinct from the island species. Moreover, its range, which extends throughout the centre of Australia, gives it the distinction of occupying the most arid habitat of any kingfisher.

The second of the three alcedinid subfamilies is the Alcedininae. These are small, blue kingfishers which can be split into two fairly clear groups. The seven species in the genus *Ceyx* are primarily insectivorous, and live in forest, often far from water; they have a dorsoventrally flattened bill, which is generally red, and often show rufous or chestnut upperparts. The 17 species in *Alcedo* feed mainly on fish or aquatic insects, and are consequently associated with water; the bill is laterally flattened and typically black, and they have blue upperparts, as well, in many cases, as a blue breastband, which is sometimes incomplete.

Attempts have been made to classify the members of the Alcedininae on the basis of the number of toes, with three toes being used for *Ceyx* and four for *Alcedo*. It is now generally agreed, however, that the number of toes is an unreliable character for indicating relationships among the alcedinids. This is because some species, such as the Silvery Kingfisher (*Alcedo argentata*) and the Indigo-banded Kingfisher (*Alcedo cyanopectus*) in the Philippines, are typical *Alcedo* species but, nevertheless, have three toes. Three species found in Australia, New Guinea and adjacent islands, the Azure, Bismarck (*Alcedo websteri*) and Little Kingfishers (*Alcedo pusilla*), were previously separated in the genus *Alcyon* because of their having three toes, but they, too, are otherwise typical *Alcedo* kingfishers. The small African kingfishers which have four toes, but which are otherwise very different from the typical *Alcedo* species, are the African Dwarf-kingfisher (*Ceyx lecontei*) and the African (*Ceyx pictus*) and Madagascar Pygmy-kingfishers (*Ceyx madagascariensis*). The first of these was previously placed in a separate genus *Myioceyx*, and the two others in *Ispidina*. These small African insectivorous kingfishers, however, are very similar in plumage and habits to forms of the Oriental Dwarf-kingfisher (*Ceyx erithaca*), which has three toes. It seems sensible, then, that they be returned to the genus *Ceyx*.

The Oriental Dwarf-kingfisher has two distinctive forms, one with a dark blue back and wings and the other lilac-rufous above. These have sometimes been treated as separate species, *Ceyx erithaca* and *C. rufidorsa*, respectively, but they hybridize readily in Borneo, Sumatra and southern parts of peninsular Malaysia and would, therefore, seem to be better treated as a single species. It is worth noting, however, that north of Kuala Lumpur they behave more like two distinct species, with little hybridization, and the red-backed form is sedentary while the black-backed form is migratory.

Three small, rather closely related African alcedinines, the White-bellied (*Alcedo leucogaster*), Malachite (*Alcedo cristata*) and Madagascar Kingfishers (*Alcedo vintsioides*), are also problematical. In several respects they appear intermediate between *Ceyx* and *Alcedo*, feeding mainly on fish and aquatic insects, but also taking some terrestrial insects, and two of the three have a red bill when adult. It is, therefore, largely a subjective choice whether to emphasize their differences and place them in a separate genus *Corythornis*, or to stress their similarities and place them in *Alcedo*. The latter course is deemed preferable here.

Isolated populations of small kingfishers on the islands of Principe and São Tomé in the Gulf of Guinea, off West Africa, have been difficult to classify. They have both been treated as subspecies variously of the Malachite Kingfisher or of the White-bellied Kingfisher. A detailed study, however, has shown the Principe population to be closer to the latter species, with the São Tomé population closer to the Malachite Kingfisher. Without the possibility of the island and mainland populations coming into contact, it is impossible to know if they are reproductively isolated. Even so, the cases of the Aru Paradise-kingfisher and the Talaud Kingfisher indicate that island forms can become reproductively isolated with only minor differences in plumage. It would seem justifiable, therefore, while recognizing that they are close to the mainland species, that these two Afrotropical forms be tentatively treated as full species, the Principe Kingfisher (*Alcedo nais*) and the Sao Tome Kingfisher (*Alcedo thomensis*).

The Variable Dwarf-kingfisher (*Ceyx lepidus*) is distributed over hundreds of islands between the Philippines and the Solomons. It certainly lives up to its English vernacular name,



The spectacular Crested Kingfisher of forest rivers and streams in the lower mountains of Asia is one of the largest members of the family. Like all kingfishers, it has a short neck, and short, fairly rounded wings with ten primaries; the shortish tail, with six pairs of feathers, is also characteristic of most alcedinids, although the long-tailed *Tanysiptera* paradise-kingfishers differ from all others in having only five pairs of rectrices.

The Crested Kingfisher is one of several species which have a distinctive crest, but in this case it really is a prominent feature, being particularly long and shaggy-looking.

When the species is seen in flight, which is heavy-looking but can be surprisingly fast for the size of the bird, the long forehead and crown feathers are normally held flat; when the bird is perched, however, it frequently raises these feathers, so that those of the forehead stand up almost vertically and the top of the bird's head appears very "untidy".

The Crested Kingfisher's barred black and white plumage, combined with its large size, is also striking, and this is reflected in the species' alternative name of Greater Pied Kingfisher.

[*Megaceryle lugubris lugubris*,  
Yoroikeikoku

(Yoro Ravine), Chiba,  
Honshu, Japan.

Photo: Tsutomu Takahashi]





with a great variety of plumages and 14 recognized subspecies. Many of these races were initially described as full species, before the wide overall range of variation in this kingfisher was properly appreciated. A good example is that of "Goodfellow's Kingfisher" from the Philippines, a form which was for some time referred to as "*Ceyx goodfellowi*", but which is now generally regarded as a part of the variable subspecies *margarethae* of the Variable Dwarf-kingfisher. The subspecies *dispar*, from Manus Island in the Bismarck Archipelago, displays considerable sexual dimorphism, the female having a largely orange head, whereas the male has a black head spotted with light blue. The sexes are alike in all other races. Moreover, some of the subspecies have a dorsoventrally flattened, red bill, in this respect resembling *Ceyx* kingfishers, while others have a laterally flattened, black bill, more like that of *Alcedo* species. It is hardly surprising, therefore, that different ornithologists have allocated the Variable Dwarf-kingfisher to either *Alcedo* or *Ceyx*. Although this kingfisher generally appears more like *Alcedo* species in plumage, it feeds mainly on insects caught in flight or on the ground and it is therefore perhaps more appropriately placed in the genus *Ceyx*.

Of the three subfamilies of kingfishers, the third, the Cerylinae, is the smallest, with just nine species in three genera. All are true fishers, and they include the only alcedinids found in America. The Cerylinae are distinguished from the other two subfamilies by lacking any blue in the plumage; they have spotted flight-feathers and several other distinguishing morphological features. The genus *Chloroceryle*, consisting of two species pairs, each with a green head and back, is restricted to the Americas. In the genus *Megaceryle* there are also four species, but they are shared equally between the New and the Old Worlds. These are the Belted Kingfisher in North and Central America and the Ringed Kingfisher (*Megaceryle torquata*) in Central and South America, while the Giant Kingfisher is found in the Afrotropics and the Crested Kingfisher (*Megaceryle lugubris*) in Asia. The Pied Kingfisher (*Ceryle rudis*) is the sole member of its genus, and occurs in Africa and southern Asia. No cerylines are found in Malesia, the region containing the highest diversity of other kingfishers.

It is suggested that an ancestral ceryline invaded the Americas from Asia in the early Pliocene, this giving rise to the genera *Chloroceryle* and *Megaceryle*. The early *Chloroceryle* initially formed one species pair, the American Pygmy-kingfisher (*Chloroceryle aenea*) and the Green-and-rufous Kingfisher (*Chloroceryle inda*), and later a second such pair, the Green Kingfisher (*Chloroceryle americana*) and the Amazon Kingfisher. These species pairs are very similar in plumage, and all four species feed primarily on fish and live in similar habitats. They could be expected to compete strongly with each other were it not for the significant size differences between them. The ancestral *Megaceryle* gave rise to the Belted and Ringed Kingfishers, and a trans-Atlantic movement of the Ringed Kingfisher gave rise to the Giant and Crested Kingfishers of Africa and Asia.

The Pied Kingfisher appears not to have any close relatives in this group, so that its origin is obscure. It is thought probable that its presence in Africa is the result of invasion by ancestral *Chloroceryle* stock from the Americas.

### Morphological Aspects

The smallest kingfisher in the world is the African Dwarf-kingfisher, weighing between 9 g and 12 g, while the African Pygmy-kingfisher weighs only a few grams more. At the opposite extreme, the largest is the Laughing Kookaburra, females of which reach a maximum of 490 g. Not much smaller than that is the Blue-winged Kookaburra, at 447 g for a female, closely followed by the Giant Kingfisher, with males which can weigh 426 g. The majority of kingfishers, however, have a weight in the range 30-100 g.

For most kingfishers, the body measurements and weights are similar for both sexes. In the few cases where the data have been analysed, either there are no significant differences between the sexes or they differ by less than 10%; in the latter

As a family, kingfishers occupy a variety of habitats, but they are often to be found by water. The little Malachite Kingfisher is widespread in Africa, where it is a common species. It is frequently observed at fresh waters, generally smaller ones such as ponds and dams, as well as slow-flowing rivers and streams, but it also occurs at tidal estuaries and mangroves. In all cases, however, it needs at least some element of fringing vegetation or rank waterside growth, such as reeds or similar plants, on which it can perch. A stem projecting well above the surrounding vegetation makes an ideal vantage point from which the bird can scan for the small fish and other aquatic animals on which it feeds. During the breeding season, this kingfisher is more likely to be seen on smaller watercourses, this presumably being due to the fact that, like almost all other alcedinids, it requires banks in which to excavate its nest.

[*Alcedo cristata cristata*, Amboseli, Kenya.  
Photo: Günter Ziesler]



The habitat that the majority of people probably associate most closely with kingfishers is rivers, be they large or small ones. This is hardly surprising, since rivers are, in fact, a favoured habitat for many members of this family, and for none more so than the Alcedo species. One of these, the Common Kingfisher, is the most familiar alcedinid in large parts of its massive Old World range, and, indeed, is the only one in most of Europe and through central Asia.

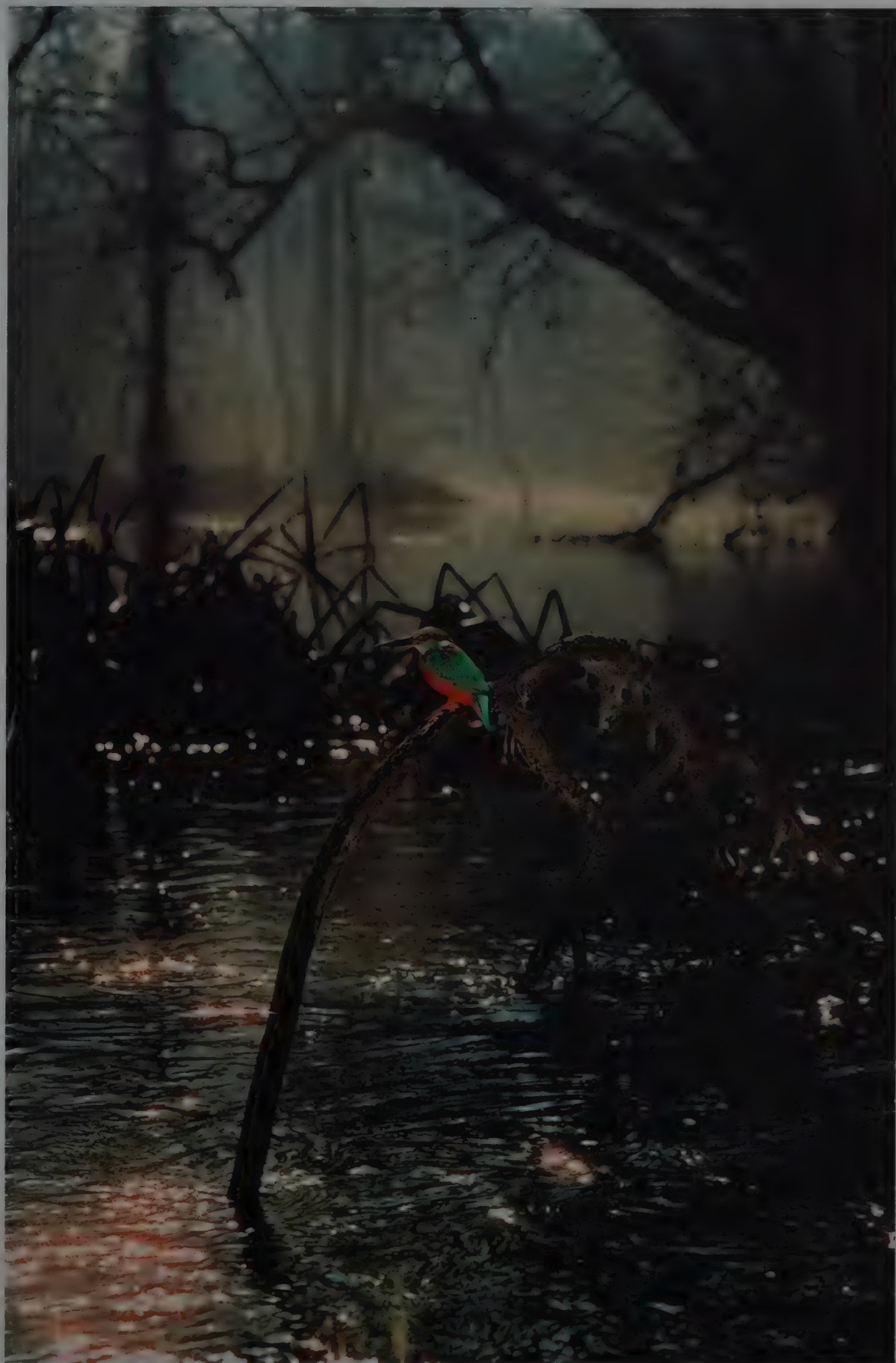
This species may be seen on watercourses of varying size, from small streams to major rivers, but it normally prefers small to medium-sized rivers with clear, slow-flowing water, and with plenty of suitably sized fish and bankside perches; it also inhabits lakes and other small, still waterbodies which satisfy the same requirements.

In winter, when inland waters freeze over, many individuals are forced to move to coastal areas, and this kingfisher can then be seen even on open rocky shorelines.

In tropical regions of South-east Asia, where Common Kingfishers face some competition from a number of similar species, they also frequent mangrove creeks, wet grassland and swamps, and it is not uncommon for them to enter large gardens. Even in Europe, where no other kingfishers are present, this species will regularly fish at ponds in quieter gardens, although, in that part of the world, it remains primarily an inhabitant of rivers and small lakes.

[*Alcedo atthis atthis*, Italy.]

Photo: Paolo Fioratti/  
Bruce Coleman]





In contrast to the relatively open river or wetland habitats used by the *Alcedo* species, many of the world's kingfishers live in forest or woodland. In fact, it is not often realized how wide a diversity of kingfishers inhabits the dense forests of the tropics. A typical species of this biotope is the Rufous-bellied Kookaburra, a common and widespread bird of the New Guinea lowlands, being generally found below 500 m. This large, conspicuously patterned species occurs in thick coastal scrub and mangroves, as well as in second growth, parkland, plantations and primary rainforest, but it shows a clear preference for monsoon and riverine forest. Here, it spends much of its time in the lower canopy, where it forages for arthropods and small vertebrates among the foliage and branches of the trees; it also nests in arboreal termitaria, the presence of which is accordingly a prerequisite for this species' occupation of a habitat. Like its congeners, however, it does descend to the ground, although only occasionally, and sometimes digs for prey such as earthworms. The rufous tail of this individual identifies it as a female, the male Rufous-bellied Kookaburra having a blue tail; both sexes have rufous underparts.

[*Dacelo gaudichaud*,  
Brown River, south-east  
New Guinea.  
Photo: Brian J. Coates]



Completely overlapping with the Rufous-bellied Kookaburra (*Dacelo gaudichaud*) in range, but at the opposite extreme in terms of size, is the tiny Variable Dwarf-kingfisher, which also extends north to the central Philippines and east to the Solomon Islands. Like the kookaburra, it inhabits rainforest and monsoon forest, but there it frequents the middle and lower strata, down to ground level. In addition, it can often be found in thick vegetation bordering streams, but, along with the other *Ceyx* species, it is no more dependent on water than is its much bigger relative.

[*Ceyx lepidus solitarius*, Brown River, south-east New Guinea.  
Photo: Brian J. Coates]



instance, either males or females are the larger, depending on the species. An exception to this generalization may be found in the Laughing and Blue-winged Kookaburras, females of which are significantly larger than males in body weight and in all other measurements. In the Buff-breasted Paradise-kingfisher, the length of both the tail-streamers and the remaining, non-elongated rectrices is significantly greater in males than in females.

In many alcedinids, the sexes are similar in plumage, too. For most members of the subfamily Alcedininae, the only difference between the sexes is that females have more red on the bill. Sexual plumage dimorphism is found only in the Indigo-banded Kingfisher, the male of which has two blue breastbands and the female a single, incomplete one, and in the Blue-banded Kingfisher (*Alcedo euryzona*), in which the female has orange underparts. By contrast, many of the cerylinae exhibit sexual differences in the pattern of the underparts. For example, the male Pied Kingfisher has two breastbands and the female has a single one, while the male Giant Kingfisher has a chestnut breast and the female has a chestnut belly. In the Belted Kingfisher, the male has a grey breastband; the female, on the other hand, has a second, chestnut breastband below the grey one, the chestnut colour extending also to the flanks. In the halcyonines, the sexes often differ in the colour of the upperparts or tail. Males of the Shovel-billed Kingfisher, as well as those of the Rufous-bellied and Blue-winged Kookaburras, have a blue tail, while the females of those species have a rufous tail. In the Banded Kingfisher, males have a blue crown, with the back, wings and tail barred blue and black; in the female, however, the entire upperparts are banded rufous and black. In the genera *Halcyon* and *Todiramphus*, the differences between sexes are slight.

Bill colours are generally black, red, or a pale yellow or brown, or some combination of these. There are few exceptions to this, these being the white bill of the Rufous-bellied Kookaburra and the bright yellow bill possessed by the two *Syma* species, the Yellow-billed and Mountain Kingfishers.

The bill of most kingfishers is long, straight and dagger-like. Those species that dive for fish generally have a bill that is laterally compressed and relatively long for the bird's body size. By comparison, those species that take prey from the ground have a

relatively shorter and broader bill. This is taken to an extreme in the forest-dwelling Shovel-billed Kingfisher, which has a very short and heavy bill which it uses for "shovelling" in the forest floor in search of invertebrates. The Hook-billed Kingfisher, which may also dig in the soil for prey, has a longer bill with a distinct hooked tip. The kookaburras also have a slight hook on the tip of the bill, and a groove before the tip provides a location for holding prey. This hooked tip is even more pronounced in young Laughing Kookaburras, which use it to attack the other siblings in the nest-chamber, this often leading to the death of the youngest. In the Mountain and Yellow-billed Kingfishers, the cutting edges of the upper mandible are serrated towards the tip. The bill of the adult African Dwarf-kingfisher is flattened, with a square tip, although juveniles have a more normal pointed tip. In some species, bill length may be reduced in summer as a result of abrasion while digging the nest-hole.

Kingfishers generally have short legs, although those species which feed on the ground have relatively longer tarsi, which give them greater mobility when hopping. The majority of alcedinids have four toes, three pointing forwards and one backwards. The inner toe is joined to the middle one for the first third of its length, and the middle toe is joined to the outer one for more than half the length. This connection of the digits is known as syndactyly. Some species in the genera *Ceyx* and *Alcedo* have only three toes, with the inner toe missing. The Sulawesi Dwarf-kingfisher (*Ceyx fallax*) has a vestigial inner toe, without a nail, and containing only a single bone.

One of the more remarkable features found within the family is the long tail-streamers possessed by the paradise-kingfishers in the genus *Tanysiptera*. These ornaments are formed by the two elongated central tail feathers, which can be up to 200 mm in length, compared with the 70-120 mm of the other tail feathers. The streamers are either white or blue, and each one terminates in a racquet-like tip in most species, although the racquets are absent in the Buff-breasted Paradise-kingfisher. The racquets exhibit the normal contour-feather structure, but the thin shafts, or "wires", leading to them have arrested development of the barbs, with the barbules lacking hooks. Recently fledged juvenile paradise-kingfishers have a long, graduated tail before they acquire the streamers of the adult plumage.



A good number of kingfisher species live along sea coasts, one of these being the Black-billed Kingfisher of Sulawesi. This large, hefty-billed, crab-eating alcedinid with a distinctive pied plumage occurs on wooded seashores and in coastal scrub, and can also be found among shrubs on sea cliffs, as well as in mangroves and estuaries; it also visits trees in coastal villages. It is not confined to coasts, however, as it extends inland along large rivers and up woodland creeks.

[*Pelargopsis melanorhyncha melanorhyncha*, Lembah Strait, north Sulawesi. Photo: Brian J. Coates/Lynx]

Both the tiny Malachite and Madagascar Kingfishers and the very large Crested Kingfisher have a distinct crest. This is periodically raised while the bird sits at a perch.

A common feature of most kingfishers is the presence of brilliant blues and greens in the plumage. These colours are not iridescent, nor are they the direct result of pigment. They are, instead, structural, resulting from what is known as "Tyndall's phenomenon". This occurs where short wavelengths of light (blues) are scattered from a cloudy medium, underlain by pigments that absorb long wavelengths (reds). In feathers, the cloudy medium actually consists of vacuolized keratin lying in the medulla of the feather barbs, with an underlying layer of melanin. Green colours are produced by a yellow filter consisting of yellow granules, and purple and violet are produced by reddish-brown granules acting as filters or situated among the light-absorbing layer. These reddish-brown granules are the direct cause of the chestnut colours often found in the ventral plumage of kingfishers. The duller greens of the American *Chloroceryle* kingfishers are a combination of general melanization (black) with intense iridescence.

Juvenile kingfishers generally have a similar plumage to that of adults, but often with duller, less striking structural colours. This is very evident in the paradise-kingfishers, where the juveniles are for the most part a mottled brown, lacking most of the brilliant blues of the adults. Juveniles of *Halcyon* and *Todiramphus* species frequently show mottling or faint barring in areas that are uniformly coloured in the adults. In the genus *Alcedo*, juveniles often have a white tip to the bill.

Chicks of most kingfishers hatch naked and blind. Later, as they grow, they retain the developing feathers in the waxy feather sheaths for a protracted period, giving them a very "spiny" appearance until the feathers break out. Pied Kingfisher chicks hatch naked, blind and pink, but by the fourth day the skin is greyish, with defined feather tracts; the eyes start to open on the fifth day, and the eyelids are well parted by the ninth. Nestlings of the Hook-billed Kingfisher are reported to have an egg tooth on both the upper and the lower mandibles, and an even more pronounced hook to the bill than that of the adult. No explanations have been suggested for these unusual features. As already mentioned, however, the hooked bill of young Laughing Kookaburras is used in siblicide.

Moulting patterns among kingfishers as a whole are quite complex and variable, but within each of the three subfamilies the patterns are more constant. In the halcyonines, the primary moult is descendant, starting with the first, innermost, primary P1. In the alcedinines, it is also descendant but starts at two loci, P1 and P7. The moult pattern of the cerylines is more variable: in the Belted Kingfisher, it is ascendant and descendant from P7, and descendant from P1, whereas in the Pied Kingfisher it is ascendant and descendant from P5. In several species of Alcedinidae the moult is slow, and it may be suspended over the non-breeding period or during migration, to be recommenced later. In the Pied Kingfisher, a new cycle of moult may start at the same time as the previous one is suspended, and some individuals have been found to retain old feathers into a third season.

The iris colour of most kingfishers is dark brown. The only exceptions are the dark red eyes of the Lilac-cheeked Kingfisher, the red or orange-red eyes of the White-rumped Kingfisher, and the white or pale yellow eyes of adult Blue-winged Kookaburras. Behind this outward uniformity, however, kingfishers have specialized eyes and, moreover, they have very good eyesight. The Sacred Kingfisher has been reported as detecting prey at a distance of up to 90 m. The retina of each eye has two foveae, which are depressions on the surface where there is an increase in the density of cone cells. The temporal fovea lies on the edge of the retina and looks out into the area of binocular vision, while the nasal fovea is located centrally, looks out into the lateral, monocular visual field, and forms a much deeper depression. In the Laughing Kookaburra, there was found to be a binocular overlap of 30°, and the projections of the temporal, binocular, foveae were nearly parallel to each other and to the bill axis. The nasal, monocular, fovea has a much greater density of retinal ganglion cells than does the temporal fovea, suggesting that, in the kingfishers, binocular vision has a minor role in resolving fine spatial details. In this family, the angle formed between the projection of the temporal fovea and the nasal fovea is particularly large, being 41-52°, and this is a result of the frontally directed projection of the temporal fovea.

Kingfishers show a limited degree of eye rotation, and, instead, they use head movement to track prey. The two foveae lie along a "horizontal streak", an area of increased ganglion-cell



One of the major reasons why the kingfishers as a group have prospered is their adaptability, as is the case with most avian families that are successful. The huge Giant Kingfisher, unmistakable within its range, which covers most of sub-Saharan Africa, is an interesting example.

Predominantly a fish-eater, but one that also takes large numbers of river crabs, it needs an aquatic habitat in order to thrive. Consequently, it can be found on large rivers and lakes having ample marginal woody growth, and at coastal lagoons, mangroves, and rocky and sandy seashores, where it sometimes hunts up to 100 m out over the water. In some places, it occurs occasionally on the stagnant pools remaining along dried-up rivers, and on rapids, in flooded woodland, and at garden fish ponds. This is one of several polytypic Afrotropical kingfishers in which, intriguingly, the habitat preferences vary according to subspecies.

In this instance, the nominate race, shown here, is a locally common bird of open woodland and savanna from Senegambia across to Ethiopia and southwards to southern Angola and the Cape. The darker and less spotted subspecies *gigantea*, however, lives in closed habitats, and is confined to the equatorial forest zone from Liberia east to Nigeria and western Tanzania and south as far as north Angola. It is considered probable that the ancestral forms of the Alcedinidae inhabited tropical rainforest, from where they have since radiated out into other habitats.

[*Megaceryle maxima maxima*,  
Okavango Delta,  
Botswana.

Photo: Pete Oxford/BBC  
Natural History Unit]





Kingfishers indulge in various kinds of comfort behaviour. Preening, which is often immediately preceded by bathing in water, is an important part of such activities. This Belted Kingfisher shows the typical attitude adopted when maintaining the condition of the flight-feathers. During this process, the wing is raised to allow the bird to reach the primary and secondary feathers and to draw each one in turn through the mandibles.

[*Megascops asio*,  
Long Island, New York,  
USA.

Photo: Tom Vezo]

density in the retina, and this streak dips  $14^{\circ}$ – $20^{\circ}$  towards the ground at its nasal end. The nasal, monocular, fovea also projects at an angle to  $7^{\circ}$ – $9^{\circ}$  below that of the binocular foveae. Similar deviations are found in owls (Strigiformes), cats and other animals that search for prey on the ground. Using a sit-and-wait hunting strategy, a kingfisher would be able to detect a food item as the image crossed its monocular fovea and then, if its head was correctly angled, a simple rotation of the head would transfer the image across the horizontal streak to the area of binocular fixation. Geometrical calculations indicate that the angle of the bill to the ground required to achieve this would be approximately  $60^{\circ}$ , and this is consistent with some field observations.

The cone cells of the retina have oil droplets containing pigments of various colours, green, yellow, orange or red, which may act as chromatic filters. The presence of red droplets has been associated with better colour vision. Kingfishers have a particularly high proportion of red droplets, as much as 60%, and this characteristic is shared with other species that hunt over water and need to see through the surface and into the water to detect their prey. The Belted Kingfisher is sensitive to near-ultraviolet light and, although the use of this is uncertain, it may be employed for navigation and prey detection.

Those kingfishers which plunge into the water for their prey have the particular problems of locating their prey and estimating its depth under water, while at the same time overcoming the difficulties of light reflection and refraction at the surface. Refraction of light causes the position of underwater prey to appear closer to the surface than it really is. These difficulties are further compounded if there is movement in the water's surface, causing fragmentation of the reflected light and the formation of dynamic lenses on the surface. Despite these many theoretical problems, however, kingfishers do successfully catch prey underwater. Laboratory experiments showed that Pied Kingfishers were able to compensate for these optical difficulties, the birds successfully capturing stationary prey in nearly all dives, at depths ranging from surface level to 45 cm under the water. As prey depth increased, the angle of dives became more vertical, and an initial slow, curved phase was followed by a relatively straight and fast descent. Further, the position at which this acceleration

phase started became higher above the water with increased depth of prey, so that the speed of the final descent increased from 2 m/s for prey on the surface to 4.5 m/s for prey 30–45 cm under the water. The kingfishers' capture rate of live, mobile prey was 50% in the laboratory, compared with a recorded capture success of 10–50% in the wild.

The Pied Kingfisher is a highly specialized kingfisher which obtains almost all of its food by diving into water. As one of its anatomical adaptations, there is a bony plate, joined to the prefrontal bone of the skull, which provides a sliding screen in front of the eye when the bird plunges into the water.

## Habitat

Just over half of the world's kingfisher species are found in forest or along forested streams, far from the rivers or lakes that most people would think of as being the typical habitat of the Alcedinidae. In fact, kingfishers occupy a very wide range of habitats, from temperate streams to coral islands and from dense tropical forest to deserts.

The most arid-adapted member of this family is the Red-backed Kingfisher. This remarkable bird is found throughout inland Australia, including the Great Sandy, Tanami, Gibson and Simpson Deserts, regions which have a mean annual rainfall of less than 25 cm and an average January temperature of over  $30^{\circ}\text{C}$ . It requires trees on which to perch in the spinifex or tussock grassland or the *Acacia* scrubland which it inhabits. Several other species, such as the Madagascar Pygmy-kingfisher and the Sacred Kingfisher, can extend into arid habitats, although much of the area of distribution of these two species lies in more mesic areas.

In contrast to the hot deserts where the Red-backed Kingfisher lives, it is cold conditions that seem to be the preferred environment of the Crested Kingfisher. This large alcedinid is found on rocky streams at up to 2800 m in northern Myanmar, and it remains at those altitudes unless the water freezes. In the Himalayas and Japan, Crested Kingfishers move down to the lower plains in winter, but in Hokkaido, the northernmost island



Halcyon species, such as the Striped Kingfisher, have distinctive, often noisy, displays in which the two partners perch near each other on a conspicuous branch and call in duet. While so doing, they spread the wings wide, thereby revealing the striking wing patches that are characteristic of this genus, and then close them again. This wing-spreading action may be repeated for some minutes. Such displays are sometimes preceded by an aerial one, in which one or both of the pair rise high in the air in circling or spiralling flight. Interestingly, the savanna-dwelling species in Africa give short, shrill calls, whereas their forest counterparts utter longer, purer notes that better penetrate the habitat.

[*Halcyon chelicuti chelicuti*, Masai Mara, Kenya. Photo: M. & C. Denis-Huot/Bios]



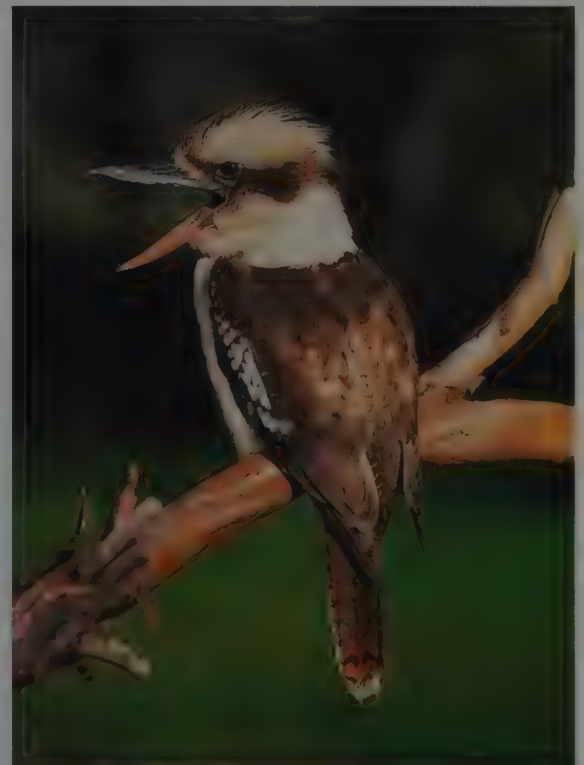
of Japan, some live around hot springs throughout the winter months, while the surrounding country becomes frozen.

A number of species are found in open woodland, often far from water. In Africa, these include the Woodland, Grey-headed, Brown-hooded and Striped Kingfishers and the African Pygmy-kingfisher. Similarly, in Australasia, the Sacred and Forest Kingfishers and the Laughing and Blue-winged Kookaburras are woodland-dwellers. Parks, gardens and cultivated lands are often not very different in structure from woodland, and so a number of kingfishers can be found in these modified habitats. Among them are the Laughing Kookaburra, and the Sacred, Chattering, Tahiti, White-throated and Javan Kingfishers.

The world's dense tropical forests are home to a great diversity of kingfishers. These are perhaps best typified by the paradise-kingfishers of New Guinea, which appear to have a predilection for primary forest and similar densely wooded habitats. Tropical forest, however, harbours many other alcedinids. These range from the large Rufous-bellied Kookaburra and Shovel-billed Kingfisher, also of New Guinea, to the medium-sized Chocolate-backed Kingfisher of Africa and the Rufous-colored Kingfisher of the Philippines, and to the tiny *Ceyx* species of Malesia and Africa. Within the forest habitat, most kingfishers are found in the lower levels, taking food from the forest floor. Somewhat surprisingly, however, the New Britain Kingfisher is more or less restricted to the canopy, apparently being excluded from the understorey by the Buff-breasted Paradise-kingfisher. In Vanuatu, its close relative the Chestnut-bellied Kingfisher, in the absence of any paradise-kingfishers, occupies all levels of the forest.

Habitat preference can vary even within a species. This is demonstrated by, for example, the African Pygmy-kingfisher and two other Afrotropical alcedinids, the Woodland and Giant Kingfishers. In each case, one subspecies is confined to forest, while the others are found in more open woodland. African kingfishers seem to have originated from invasions by forest kingfishers, either from Malesia or from the Americas (see Systematics), and it is likely that the forest-inhabiting subspecies are closer to the ancestral types, which have subsequently radiated into the savanna woodland of the Afrotropics.

Clearly, the kingfishers that obtain their food by fishing require an aquatic habitat. Suitable waters can vary from small streams and rivers, as used by many of the *Alcedo* species, to large rivers and lakes, which are exploited by the Giant, Ringed and Belted Kingfishers. Belted Kingfishers have been recorded up to 1 km offshore, but the specialized feeding behaviour of hovering has allowed Pied Kingfishers to move out even farther.



Few bird voices are as famed as that of the Laughing Kookaburra, which derives its vernacular name from the extraordinarily loud, cackling chorus given by a pair or a group of these huge kingfishers. This "laugh", heard mainly at dawn and dusk, is, in fact, a complex sequence of five different elements, the final one of which is sex-specific. Apart from the last one, some of the elements may be omitted, and the sequence itself can vary. Moreover, the individuals do not utter their calls in synchrony, and the result can be a wild cacophony of sound, well known to inhabitants of the Australian bush.

[*Dacelo novaeguineae*, Australia. Photo: Dave Watts]

The latter species has been recorded well out from the coast on the Red Sea, and even as much as 3 km from land on Lake Kariba, on the Zambia-Zimbabwe border in southern Africa.

Many species of kingfisher are also found along sea coasts, taking prey from the marine environment. The most widespread of these is the Collared Kingfisher, which is closely associated with mangroves in some areas. On islands in the Pacific, its habitat selection seems to be influenced by competitors: if similar kingfishers are present on an island, then the Collared Kingfisher is confined to the coastal fringe, but it moves inland, into forest, if there is no competition from other alcedinids. The Beach Kingfisher also feeds from the mangroves, and at low tide it will move several hundred metres offshore. It seems to provide competition for the Collared Kingfisher along the coast, as evidenced by the observation that, where one species is common, the other is generally rare.

Some species show habitat shifts associated with post-breeding migration. One such example is that of the Mangrove Kingfisher on the east coast of Africa. This species spends its non-breeding season in coastal mangroves, but it moves 5-50 km inland to breed in woodland. Similarly, in much of Europe, many Common Kingfishers move to more open coasts for the winter, since the inland lakes and rivers on which they breed often freeze over during the latter season.

Much of the success of kingfishers in spreading around the world can be attributed to their ability to adapt to a wide range of habitats. Their ancestral forms probably inhabited tropical rain-forest in Malesia, and they have since radiated to occupy most available habitats. Even so, the relatively small number of alcedinid species in Europe and the Americas occupy a more limited range of habitats.

### General Habits

Many kingfishers are solitary except when breeding, but some, such as the Laughing and Blue-winged Kookaburras, are commonly found in groups of up to eight individuals, these consisting of a pair and its offspring from previous years. Kingfishers are highly territorial, defending both breeding and non-breeding territories. In winter, the male Common Kingfisher usually de-

fends the same territory as that which he used for breeding, while the female's territory is nearby or is partly shared. During hard winters, the density of birds at good feeding sites may greatly increase, as was found in Hungary, where there were more than seven Common Kingfishers per kilometre of river. In Australasia, territories of the Blue-winged Kookaburra were defended throughout the year. The average size of 26 such territories was 0.4 km<sup>2</sup>, and some of these overlapped the territories of smaller species of kingfisher. Where Laughing and Blue-winged Kookaburras occurred together, however, their territories were mutually exclusive. When not breeding, Pied Kingfishers defend favoured perches and the area around them; when food is scarce, they attack other birds which are in flight, and there may be tussle in mid-air over fish being carried back to a perch.

Sacred Kingfishers are very aggressive towards a wide range of birds in their breeding territory. They utter the "Attack Screech" (see Voice), and sometimes strike intruders with the bill. Other bird species attacked by this kingfisher range from Common Starlings (*Sturnus vulgaris*) and House Sparrows (*Passer domesticus*) to Silver Gulls (*Larus novaehollandiae*) and White-faced Herons (*Egretta novaehollandiae*). One adult repeatedly hit a Laughing Kookaburra on the neck. They will also attack goannas (*Varanus*), weasels (*Mustela nivalis*), stoats (*Mustela erminea*), dogs and cats that come near their nests, and there are reports of cats and dogs being blinded, or even killed, by these assaults. Common Paradise-kingfishers have been seen attacking several other species, including a Red-necked Crake (*Rallina tricolor*), a Hooded Pitta (*Pitta sordida*) and a Greater Black Coucal (*Centropus menbeki*). Forest Kingfishers mob passerine birds, especially those feeding on the forest floor, such as Magpie-larks (*Grallina cyanoleuca*), and one was once seen to launch a violent attack on a Varied Triller (*Lalage leucomela*), both birds falling about 18 m to the ground while locked together.

Most kingfishers forage during the day. Studies showed that Pied Kingfishers were active during four periods of the day, with quiet intervals in between during which a pellet was produced, but on Lake Kariba, in southern Africa, that species modified its active period to match that of an introduced sardine (*Limnothrissa*), which fed at the surface at dawn and dusk (see Food and Feeding). The White-throated Kingfisher is generally most



It seems that most kingfishers have a limited range of fairly simple calls. The Ringed Kingfisher of the Neotropics, for instance, utters a loud "kleck", sometimes repeated, and a rattling alarm call of similar notes. The vocalizations of the majority of alcedinids, however, have not been studied to any great extent, and it is quite possible that many, or even most, of them have a far wider range of calls. This has proven to be the case for those few species that have been more fully investigated.

[*Megascops torquata torquata*, Pantanal of Brazil.  
Photo: Günter Ziesler]



The calls of the forest-dwelling paradise-kingfishers of New Guinea are rather different from those of most other kingfishers. The main call of the Common Paradise-kingfisher consists of up to four evenly pitched long, low, mournful whistles that accelerate into a trill; a similar protracted whistle is also given singly, either upslurred or downslurred. Harsh chatters and shrill squawks, sometimes emitted in flight, and presumably having more of an alarm function, are also part of this species' vocabulary. The conspicuous white rump and tail-racquets of this handsome kingfisher are seen well in this shot.

[*Tanysiptera galatea minor*,  
Brown River,  
south-east New Guinea.  
Photo: Brian J. Coates]



active at dawn and dusk, with a distinct midday lull when it shelters from the heat of the day in palm trees. In Iraq, these kingfishers have been seen foraging for flying beetles for more than an hour after dusk. Similarly, in America, the Belted Kingfisher is also least active around noon. The Blue-winged Kookaburra, too, forages most actively at dawn and dusk and in the early hours of the morning, being quite inactive during the heat of midday. Like the White-throated Kingfisher, it will also make use of street or security lights to forage long after dark.

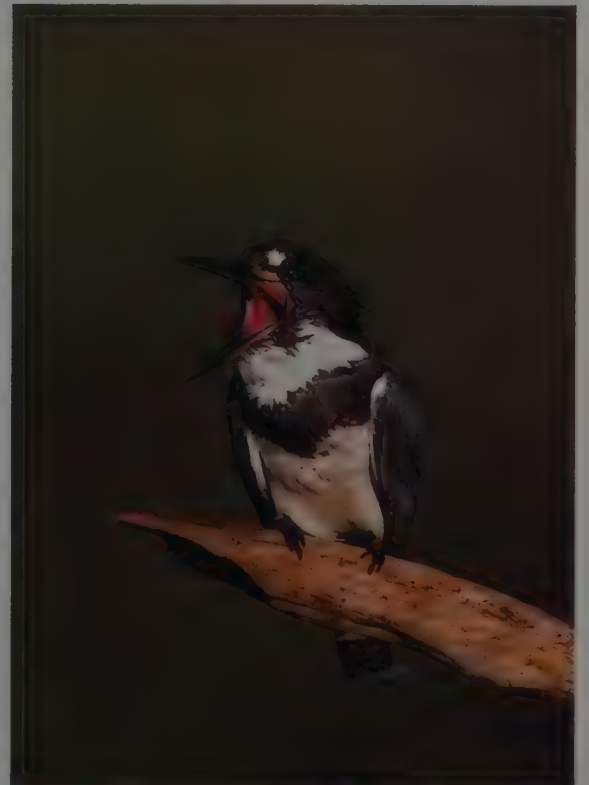
In contrast to all other alcedinids, the Hook-billed Kingfisher is crepuscular and nocturnal. It starts to call just after dark and can continue throughout the night, with a peak in vocal activity just before dawn. When breeding, it is more active by day, and will also call then during the daylight hours.

Many kingfishers bathe by dipping in and out of the water, after which they move to a loafing site, such as a shady tree, in order to preen. White-throated Kingfishers dip from a low perch into a shallow pool to bathe. They return almost immediately to the perch, where they vigorously shake themselves and wipe the bill on the branch, but they do not then preen. This action may be repeated four or five times. The Variable Dwarf-kingfisher also dives into the water several times until it becomes soaked, and then it preens. The Common Kingfisher bathes frequently, particularly after nest-building, copulation, nest-relief, feeding of the young, and capture or attempted capture of prey. This well-known alcedine probably preens for a total of about two hours in each day, in six to eight bouts, diving into the water several times and preening in between, then yawning, stretching and flying off. While preening, it may use the underside of the wing to rub the top of the head, a very unusual action among birds. Laughing Kookaburras use a similar action for transferring uropygial oil to the head.

The Blue-winged Kookaburra bathes in this same manner, by diving into water, and then returns to a perch to preen. It also preens at the roosting site, and after having spent some time in the nest, as well as during periods of rain. In the process of preening, this large kingfisher draws the feathers of the underparts, back, rump and wings through its bill, and may scratch several parts of its head. The bill may be wiped on each side of the branch, this action being followed by a rapid shake of the head and bill, producing a loud bill-rattle which sounds like castanets. As part of preening, it often stretches one wing out and down and then does the same with the other wing, before stretching the body

forward with the wings partly raised. These kookaburras sometimes sun themselves, either on a branch or on the ground, assuming a bizarre posture with the head held at a peculiar angle and one wing extended. In hot weather, they hold their wings out and slightly down from the body, and gape with the bill wide open. In addition, anting has been reported for the Blue-winged Kookaburra in north Queensland.

The Common Paradise-kingfisher seldom bathes. On those few occasions when it does so, it performs this activity in the same way as do other kingfishers, by diving into water.



Detailed studies of several kingfishers have revealed that these have a wider range of vocalizations than was previously realized. One of the better-studied alcedinids is the Belted Kingfisher of North America. This species has been found to have a number of calls, ranging from screams to rattling and mewling sounds, and even to what have been termed "warbling" calls. These different vocalizations are used to convey different messages, and slight variations in the calls, or combinations of two types, provide additional information to conspecifics.

[*Megaceryle alcyon*,  
Long Island,  
New York, USA.  
Photo: Tom Vezo]



Although a very small number of kingfisher species forage on the ground, the vast majority of the members of the family are exclusively still-hunters that forage by watching from a perch, whether they are seeking terrestrial prey or aquatic ones. In south Asia, the Brown-winged Kingfisher keeps watch from a branch fairly high up in the mangrove forest. On sighting a crab on the mud, it drops down and flies low over the ground to seize the crustacean; if it spots a fish in the shallows, it plunges directly into the water to capture it. In Australia and New Guinea, the little Azure Kingfisher, just half the size of the Brown-winged, has a diet consisting almost entirely of small aquatic animals. This species, one of the classic fishers among the Alcedinidae, obtains almost all of its food by plunging from a low waterside perch into the water; similarly, the occasional spider or orthopteran that supplements its diet is taken after a short drop or dive to the ground.

[Above:  
*Pelargopsis amauroptera*,  
south-east Sundarbans,  
Bangladesh.  
Photo: Gertrud &  
Helmut Denzau.



Below:  
*Alcedo azurea ruficollaris*,  
Kakadu National Park,  
Northern Territory,  
Australia.  
Photo: David Hosking/  
FLPA]



Several kingfishers use hovering as a foraging technique, but in none is this behaviour better developed than it is in the Pied Kingfisher. Although this attractive piscivore will hunt by scanning from a perch, it obtains a large percentage of its food by hovering persistently on rapidly beating wings while keeping a careful eye on the water below.

This ability to hover for prolonged periods means that it does not need to return to a perch, a fact which has enabled this species to exploit additional feeding niches far out from the shore. Nevertheless, it must still return to a perch with larger fish, which have to be beaten before being swallowed.

[*Ceryle rudis rudis*,  
Masai Mara, Kenya.  
Photo: Jonathan Scott/  
Planet Earth]



Perhaps rather surprisingly, there appear to be very few accounts of play among kingfishers. Laughing Kookaburras sometimes take objects such as spaghetti or string beans and beat them incessantly on a perch as they would real food, but it is difficult to say whether this could truly be described as play.

Most members of this family roost at night in trees or shrubs within the territory. Common Kingfishers roost alone in dense bushes or trees near the water, and in the breeding season this is often some distance from the nest. In winter, they will occasionally roost in an old nest-tunnel. Belted Kingfishers generally roost in large trees, often at the end of slender branches, so as to avoid predation, although males, during the breeding season, may roost in burrows near the nest-site. Buff-breasted Paradise-kingfishers roost singly at night, sitting on a horizontal branch, close to the trunk, often in the forest canopy. In Asia, White-throated Kingfishers have been found roosting overnight with their recently fledged young in the nest-tunnel.

Blue-winged Kookaburras roost on horizontal branches in the canopy foliage of tall trees. These night-time roosts are significantly higher than the diurnal perches utilized for foraging, and the same site can often be used repeatedly. The kookaburras perch horizontally, with their underparts resting on the branch, unlike the more upright perching position that is assumed in the day. They arrive at the roost about 30 minutes after sunset, around the time of the evening chorus, and leave about 30 minutes before sunrise, again during or after the morning chorus. The breeding partners usually roost within a metre of each other, with the helpers (see Breeding) nearby or in an adjacent tree. During incubation and brooding, the female will generally roost in the nest-chamber. A group of Laughing Kookaburras usually roosts communally, but sometimes splits into small subunits. Several favourite trees are used sequentially by the group.

Adult and immature Pied Kingfishers roost together at night, using fallen trees, date palms, papyrus swamps, and unused nest-holes. Night-time gatherings of over 200 of these birds are reported from Uganda, where the numbers using the roost increased after the breeding season ended. Most birds arrive at the roost-site 20 minutes before sunset. The Grey-headed Kingfisher also shows some tendency to sleep communally at night after breeding, with 24 found roosting together in a large tree in Nigeria.

There are relatively few accounts of adult kingfishers falling prey to other animals. Their fast flight probably allows them to elude most avian predators. One report details the reactions of a Pied Kingfisher which was attacked by one of a pair of Lanner Falcons (*Falco biarmicus*). After two attempted strikes in the air, which the kingfisher evaded by rolls and somersaults, it avoided a third stoop by hitting the water with a splash and submerging. Three more times the Lanner stooped, and on each occasion the kingfisher submerged, apparently becoming more exhausted each time, until finally the Lanner caught the kingfisher as it fluttered out on to the mud. Adults and fledglings of the Forest Kingfisher often fall prey to one of the smaller falcons, the Australian Hobby (*Falco longipennis*).

The Laughing Kookaburra has been reported as among the prey of Whistling Kites (*Haliastur sphenurus*), Wedge-tailed Eagles (*Aquila audax*), Peregrine Falcons (*Falco peregrinus*), and Powerful (*Ninox strenua*) and Barking Owls (*Ninox connivens*). In Northern Australia, the Red Goshawk (*Erythrotriorchis radiatus*) is the main threat to recently fledged young and adults of the Blue-winged Kookaburra, and some pairs of this goshawk seem to specialize on the kookaburra. In addition, there is an instance of a marsupial, the northern quoll (*Dasyurus hallucatus*), killing an adult Blue-winged Kookaburra at a night roost. In New Guinea, a Bare-eyed Rail (*Gymnocrex plumbeiventris*) suddenly rushed at a Common Paradise-kingfisher that was foraging on the forest floor; a scuffle took place, but the kingfisher managed to escape and fly off to a low perch.

When Belted Kingfishers detect an intruder in their territory, they fly to a nearby perch, lift the body up and down, raise the shaggy crest, and give the shrill rattle call (see Voice). Interactions between raptors and Belted Kingfishers are of two kinds. There are cases whereby the raptor, such as a Cooper's Hawk (*Accipiter cooperii*) or a Northern Goshawk (*Accipiter gentilis*), initiates the chase with predatory intent, and juvenile kingfishers, in particular, often fall victim to these attacks. Adult kingfishers try to evade the raptor by diving into the water. There are other cases in which the kingfisher, on becoming aware of a raptor, often a Cooper's Hawk, in its territory, gives its rattling call and flies directly at the predator, which then gives chase, with the kingfisher dodging between trees until the hawk gives up. These



Kingfishers are patient hunters, often sitting for lengthy periods at a favourable-looking spot, occasionally bobbing the head or flicking the tail. When they catch sight of a suitably sized prey animal, however, the reaction is immediate. This Blue-eared Kingfisher is on the point of launching itself from its perch, the open wings providing the initial momentum for a steep and rapid downward plunge. Shown to advantage here, incidentally, is the closely dark-barred blue crown, a characteristic plumage feature of the genus *Alcedo*.

[*Alcedo meninting meninting*, Cigenter River, Ujung Kulon National Park, west Java. Photo: Mary Plagel/Bruce Coleman]

approaches and chases may be repeated several times until the raptor leaves the territory, and they seem to be a case of predator-mobbing rather than play. Pied Kingfishers have also been seen to chase and mob Western Marsh-harriers (*Circus aeruginosus*).

The Yellow-billed Kingfisher, when alarmed, raises its head feathers so that the two black nuchal spots are made very conspicuous, and resemble two large, staring eyes. H. L. Bell once walked around a sitting bird which kept these "eyes" directed at him, making him think that this behaviour was mimicry of a large, and possibly dangerous, animal. Almost as striking, in a different way, is the anti-predator response of young Red-backed Kingfishers. When, in the arid scrub and dry woodland of Australia, the adults of that species utter an alarm call, their fledglings adopt a cryptic pose, closing their eyes and pointing the bill upwards, so that the dark bill and the dark eyestripe form a line with the dark wings and back, looking very like the limb of a tree. Similar behaviour is seen in the Forest Kingfisher.

Small passerine birds have been seen mobbing both Common and Buff-breasted Paradise-kingfishers, and they frequently mob Laughing and Blue-winged Kookaburras. In the case of the kookaburras this mobbing is justified, because both species occasionally feed on young birds.

## Voice

The bright plumage of most species of kingfisher would suggest that visual, rather than aural, communication would be most common in the family, and that many of the less colourful species have the more elaborate calls.

For the Common Kingfisher, the best known of the alcedines, seven different calls are documented, but these are mainly variants of the "tit tit" contact-alarm. A song, with a richer variety of whistles and warbles, is sometimes given by males, or by both sexes in courtship. A song has also been recorded from the Malachite Kingfisher; given in duet, it can be transcribed as "ii-tii-cha-cha, chui, chui, tuiichui, chui", and ending with a chuckle. The calls of young Common Kingfishers change with age. Newly

hatched chicks have a plaintive "peep", but around ten days of age the food-begging call becomes a loud purring "uurr uurr", audible at a considerable distance from the nest; near to fledging, this becomes a harsh growling "gred gred". For most of the other alcedines, however, the only call reported is a high-pitched "zeeet", which may be repeated, as they fly off down a river. This probably serves as a contact or alarm call.

Most of the cerylines also have simple calls, usually a repeated "tek tek tek". Those of the smaller species are quiet, but the vocalizations of the Amazon Kingfisher are loud and harsh. The Pied Kingfisher has complex social habits, and accordingly it has a variety of calls. These include loud advertising calls sounding like "chickkerker", aggressive "shreer" calls, appeasement and begging calls, and others. The calls of its young also exhibit changes with age.

The well-studied Belted Kingfisher has several different vocalizations, associated with different messages. These have been described as "scream", "harsh", "rattle", "mew" and "warbling" calls. Scream calls are associated with non-aggressive behaviour, as when retreating from a threat or in a defensive threat, as well as in greeting, or when a mate approaches. Harsh calls are given by the male early in the breeding season in disputes with other males. Rattle calls are heard in a variety of situations, particularly territorial disputes and when humans enter a pair's territory. The warbling call is given by females when soliciting copulation, and before courtship feeding, and by males when feeding older nestlings. Mew calls are given after copulation, and during chases by the pair over its territory. Combinations of these different vocalizations can provide additional information. For example, the combination of the harsh call and the scream call is used by a male to attract females. Even relatively subtle changes to these calls can be used to vary the message conveyed. Rattle calls, which normally consist of a series of single pulses, have a higher proportion of double or triple pulses when the vocalist is more aggressive.

Many of the forest kingfishers, the halcyonines, are very vocal. Their loud, distinctive calls are used to advertise the territory, particularly during the breeding season. There is often a peak in calling around dawn, the Shovel-billed Kingfisher, for



Depending on the precise location of the prey, a diving kingfisher either snatches the item from the surface or plunges more deeply. In the latter case, it will submerge fully and continue for a variable distance under the water. The Common Kingfisher, which in many parts of its vast Old World range feeds primarily on small fish, frequently disappears briefly beneath the surface. As it nears the water, it draws in its wings until they are about half closed and, on entering, it extends them backwards to produce a streamlined shape. When submerged, it uses the protective nictitating membranes to cover its eyes, and quickly grabs the fish before it can escape. Using the natural buoyancy of its body, in combination with one or two beats of the wings, the kingfisher rapidly returns to the surface and rises more or less vertically from the water; it then immediately returns to a perch, to deal with its catch in the appropriate manner. It is interesting to note that this species is so well adapted to this plunging technique that it has even been known to dive straight through thin ice in order to capture its food.

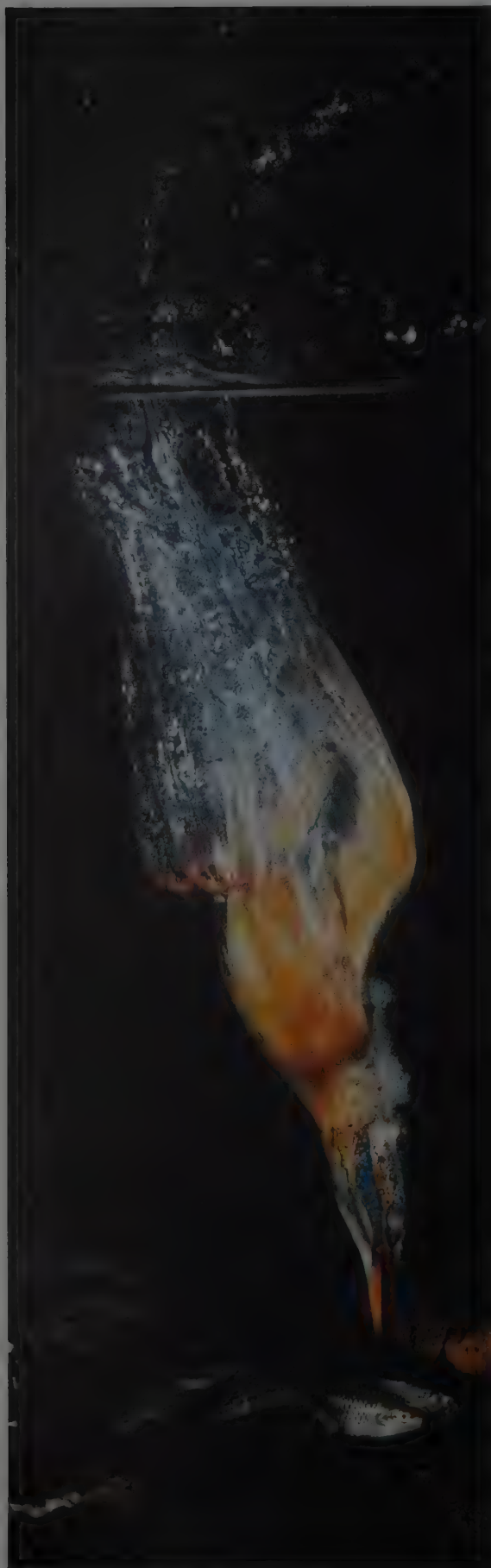
[Above left:  
*Alcedo atthis atthis*,  
Italy.  
Photo: Paolo Fioratti/  
Oxford Scientific Films.

Above right:  
*Alcedo atthis ispida*,  
Podji National Park,  
Czech Republic.  
Photo: Zdenek Tunka/  
Ardea.

Below left:  
*Alcedo atthis atthis*,  
Italy.  
Photo: Paolo Fioratti/  
Bruce Coleman.

Below right:  
*Alcedo atthis atthis*,  
Italy.  
Photo: Paolo Fioratti/  
Planet Earth]





example, giving three or four clear notes from near the top of a tall tree just after dawn. Other halcyonines, such as the Laughing Kookaburra, have a second peak at dusk. An exception to this general pattern of vocal activity is the Hook-billed Kingfisher, which calls and sings mainly at night.

Species of *Halcyon* have loud, characteristic territorial calls, often delivered from a conspicuous perch. The White-throated Kingfisher calls from a treetop, sitting upright and occasionally spreading its wings to show the white patches on the underwing. One was watched performing a display-flight, in which it flew up to 60 m, calling loudly, and then spiralled back to the trees. The Grey-headed Kingfisher also has a display-flight: pair-members circle, calling loudly in the air, and then settle on a high branch, both continuing to call and flicking their wings open to show off the wing spots. The Woodland and the Striped Kingfishers have similar displays, the male and female duetting with trilling calls and wing-spreading.

The African *Halcyon* kingfishers also provide a good example of how the call has been adapted to the environment. Those species inhabiting open savanna habitats utter short, shrill notes with many harmonics, while those living in forest have long, pure, descending notes which can penetrate the habitat more readily. Kingfishers living along streams and rivers have to contend with a continuous low-frequency background noise from the water. Calls higher than 1.5 kHz seem to be unaffected by this background noise, and the series of higher-pitched pulsed calls of many aquatic kingfishers may be an adaptation that enables the voice to penetrate through the noisy background.

One of the best-known songs of all the kingfishers is that of the Laughing Kookaburra. This species' voice is one of the most familiar sounds of the Australian bush, but its "laugh" is actually quite complex, conveying a considerable amount of information. The laugh consists of five elements: "kooa", "cackle", "rolling", "haha", which is the laugh, and "gogo" or "gurgle". The last element is sex-specific, males giving the "gogo" and females the "gurgle"; some of the other elements may be missing, and the sequence can be variable. Laughing Kookaburras are found as pairs, or in small groups with a number of non-breeding helpers. The laugh is usually given as a chorus of the pair or by all members of the group, but it is not synchronized, so that different elements may be given at the same time. The chorus of a group lasts longer, and has more of the loudest "haha" elements, than does that of a pair. These choruses are uttered throughout the year, but they are most frequent prior to the breeding season and are least frequent immediately after breeding, when the birds are moulting. They are given mainly at dawn and dusk at the roosting site, with all members of the group joining in. The dawn chorus of one group is followed by choruses from neighbouring groups, and this indicates the location of adjoining groups and assists in defining the territories. Occasionally, choruses are given on moonlit nights.

During the day, a kookaburra chorus is usually initiated by the breeding male starting the song, whereupon the breeding female flies to him and completes the chorus. Other daytime songs are usually associated with territorial disputes between groups or within the group. A daytime song by a helper indicates a challenge to the breeding male's position. Thus, the laugh reflects aggression in territorial defence, mate-guarding and maintaining the status of breeders over helpers. Young birds attempt to laugh six weeks after fledging, and are competent vocalists after a further six weeks.

Some elements of the laugh can also be given independently. For example, a deep, guttural "kooa" warns of the presence of birds of prey, a softer version gains the attention of other members of the group, the cackle is used before an attack, and the rolling or gurgle, also called a "chuckle", is a contact call used when relieving an incubating bird or when feeding young. There are also two unrelated calls. The first is a "squawk", used by adults begging for food, or as a submissive call, reducing aggression among the group during the breeding season, or in a softer version as a courtship call. The second is a "screech", used during fighting.

The Blue-winged Kookaburra has a similar chorus, which is also complex in structure, and which is given by members of the

*The hydrodynamic streamlining of the kingfisher's body shape as the bird enters the water is perfectly demonstrated here. By pulling its wings right back in this way, and at exactly the right moment, the Common Kingfisher succeeds in reducing to a minimum the resistance of the water; this permits it to travel at speed directly to its intended prey, which it can thus take by surprise. This photograph also gives a good idea of the way in which the nictitating membrane is employed. Often referred to, perhaps somewhat misleadingly, as the "third eyelid", this transparent fold of skin is situated beneath the real eyelid, and can be drawn across the eye. Many vertebrates, including all birds, possess this membrane, one of the functions of which appears to be to clean or moisten the corneal surface while at the same time the animal retains adequate vision. The nictitating membrane also protects the eye in a variety of situations, as when, for example, a kingfisher dives into water.*

[*Alcedo atthis*.  
Photo: Silvestris  
Fotoservice/NHPA]



In the cold rivers of its upland habitats in south and east Asia, the Crested Kingfisher survives on a staple diet of fish and crayfish. Although some six or seven times bigger than the far more widespread Common Kingfisher (*Alcedo atthis*), it is nevertheless very similar to that species in its foraging behaviour.

From a perch on an overhanging branch, or a rock or partly submerged log, it dives into the water with a splash, seizes a fish in its open mandibles, and returns directly to its perch. As is normal among the members of this family, the prey is held crosswise in the bill. Unsurprisingly in view of its large size, the Crested Kingfisher takes relatively big fish, mostly 15-18 cm in length, and it tends to plunge at a more oblique angle than do many of the smaller alcedinids. It prefers smaller rocky or gravel-based streams and rivers with fast-flowing water, and will return repeatedly to favoured stretches of particular watercourses. It is interesting that this hardy species, which lives at altitudes of up to 2800 m, seems to prefer the cold conditions that prevail there. Even during the winter months it descends to lower levels only when the water freezes, and on Japan's northernmost island of Hokkaido, where the winter climate can be severe in the extreme, it is able to get by during that season by remaining around hot springs.

[*Megaceryle lugubris lugubris*, Yoroikeikoku (Yoro Ravine), Chiba, Honshu, Japan. Photos: Tsutomu Takahashi]





Having successfully caught a fish, this Common Kingfisher is about to alight, feet first, on a nearby stump. This photograph shows to advantage the particularly short legs and rather sturdy feet possessed by the majority of kingfishers. The toes are also rather short, while the claws, although fairly narrow and not especially long, are nevertheless very sharp, which makes them ideal tools for gripping a perch. Less aquatic species tend to have proportionally longer and stronger legs and feet, in connection with their more terrestrial foraging habits.

[*Alcedo atthis ispida*, Río Adaja, Avila, Spain. Photo: José Luis Rodríguez/Nature & Travel]

group, particularly at dawn and dusk. The other species of kookaburra, too, have loud territorial calls, but they have not been studied in such depth.

Detailed studies of wild and captive Sacred Kingfishers revealed that they had a much wider range of calls than had previously been realized. In addition to the territorial "Staccato Call", transliterated as "kek kek kek", which is given mainly by the male from an exposed perch, several other loud calls were identified. These were an "Ascending Roll", given as a greeting when approaching a mate, a "Shriek", emitted mainly by the female to attract attention, an "Attack Screech" when attacking predators, and a "Predation Scream" when caught by a predator. These kingfishers also possessed a group of soft vocalizations, in the form of screeches, whistles and chirps, that were much quieter and were often combined into a complex call, given either at night or when the birds were in the nestbox during the day. The most common pattern was a form of duetting in which two birds in a nestbox combined a series of soft calls.

An analysis of the territorial staccato calls uttered by a population of Sacred Kingfishers showed that readily identifiable differences existed between individuals, and that these differences remained constant for at least one year. If such individual differences in vocalizations are found to be present in other kingfisher species, this could provide a useful technique for monitoring the populations of endangered alcedinids.

The Belted Kingfisher gives a pulsed call when it approaches its nest in which a partner is incubating. In an elegant experiment, using a heart-rate monitor located beneath the eggs, it was demonstrated that the cardiac response of the incubating bird when it heard the approach call of its mate differed from its response to that of an unfamiliar bird. It seems that temporal differences in the initial few pulses of the call, rather than differences in pitch, were the basis for this individual recognition.

Several kingfisher species produce non-vocal sounds. After preening, Laughing and Blue-winged Kookaburras sometimes shake the head so violently that the bill makes a rattling sound. Similarly, the Sacred Kingfisher, after eating or preening, will also shake its bill so that it sounds like soft castanets, and when swooping at intruders it makes a loud bill-snap.

While it seems that most members of the Alcedinidae have a small range of relatively simple calls, this may well be because

the majority of them have not been studied to any great extent. Detailed studies of a few species, particularly the halcyonines, have revealed, however, that these have a much wider range of calls, which are important in a variety of social interactions. It is likely that further research will show that this is true of many more species of kingfisher.

## Food and Feeding

The idea that kingfishers eat nothing but fish may seem a reasonable assumption, but it would be very far from the truth. Certainly, many kingfishers do catch fish, and some specialize in this prey, but most members of the family take a much wider range of foods. A good example of this is the Sacred Kingfisher, a common and well-studied species found in the woodland of Australia, New Zealand and islands to the north. It has been reported as taking a very wide range of animal prey, comprising annelids, molluscs, crustaceans, centipedes, spiders, insects, fish, amphibians, reptiles, birds and mammals. Apart from marine groups, there is hardly a major animal group missing from this list. The White-throated Kingfisher in Asia has a similarly wide range of food items, but there is some evidence that individual birds or populations specialize in particular food types and avoid others; thus, some birds feed on terrestrial prey and do not take fish, even though fish are readily available.

Other kingfishers have a much more delimited diet. In many localities, the Common Kingfisher feeds primarily on small fish, taking just the occasional aquatic insect, mollusc, crustacean or amphibian. A detailed study of five South American kingfishers found that they, too, fed mainly on fish, supplemented now and again with an aquatic invertebrate. In this most interesting study, two of the five species, the American Pygmy-kingfisher and the Green-and-rufous Kingfisher, were found mainly in shady habitats, such as forested streams and flooded forest. The other three, the Green, Amazon and Ringed Kingfishers, occurred mainly in open habitats, along the edges of streams and lakes. The sites where all five kingfishers were present had much higher densities of surface-dwelling fish than did those where only the three larger species were present. The birds' predation on the surface fish was proportional to the abundance



As demonstrated by this Pied Kingfisher, the fish is held crosswise in the bill ready for treatment. In this photograph, the potentially dangerous spine of the prey is clearly visible. This widespread alcedinid eats a good variety of fish, and seems able to adapt to whatever fish species is most abundant at a locality at a particular time.

[*Ceryle rudis leucomelanura*,  
Bharatpur, India.  
Photo: Jean-Louis  
Le Moigne/Bios]



of the fish in the habitat, with no indication of selection for or avoidance of any group of fish. On no occasion, however, did they take one common species of surface fish, *Cichlasoma festivum*, possibly because of its large eyes and its superior ability to avoid surface predation. The density of kingfishers at different sites was correlated with the density of surface-swimming fish, with the availability of suitable perches being of lesser importance. These five species of kingfisher differed considerably in body size, and this was reflected both in their fishing behaviour and in the size of prey that they caught. The larger kingfishers, the Green-and-rufous, the Amazon and the Ringed, used higher perches than did the smaller species, but the majority of their dives were made within 1 m of the shore, and nearly all within 2 m of the shore, which was where the density of surface fish was the highest. The size of the individual fish caught was closely related to the size of the kingfisher and to its bill length. At sites where the densities of fish, particularly of larger fish, were low, however, the larger kingfishers caught a greater proportion of smaller fish.

For captive Belted Kingfishers with a mean body weight of 130 g, the average daily energy consumption was 55-61 kcal, and this varied little across the year, despite changes in temperature, daylight and activity cycles. The smaller Malachite Kingfisher takes large numbers of small fish. At Lake Naivasha, in Kenya, one ate 15-20 small *Tilapia grahami* each day; the number doubled when it was breeding, and the five nestlings were fed an additional 60-70 fish each day.

Most woodland and forest kingfishers feed on invertebrates. Grasshoppers are a frequent part of the diet of alcedinids ranging in size from the tiny African Pygmy-kingfisher to the much bigger Laughing Kookaburra, but many other insects are eaten as well. The emergence of flying termites provides an abundant and rich source of food for many types of bird, including many species of kingfisher. Crabs can also provide an abundant food source, although their capture can be difficult. The Stork-billed Kingfisher, along with its allies, has a very long bill in relation to its body size, and this may be particularly useful for dealing with crabs on mudflats, where these crustaceans form a large part of its diet. In one observation, a Madagascar Kingfisher was seen to use its bill to prise crabs from their shelter as they hid in crevices in a small cliff face.

Several kingfishers take terrestrial vertebrates. The Beach Kingfisher, after feeding mainly on crabs at low water, moves at high tide into coastal vegetation, where it catches lizards and insects; indeed, its specific name, *saurophagus*, means "lizard-eater". The Laughing Kookaburra is also a renowned killer of snakes and lizards. It consumes snakes up to 1 m in length, first gripping them firmly just behind the head, and then bashing them violently on the ground or on a perch, before swallowing them head first.

Red-backed Kingfishers of central Australia have been recorded attacking the nesting colonies of Fairy Martins (*Hirundo ariel*). A pair of these kingfishers took turns in flying up to the mud nests, pecking away at the nest-tunnel until it broke off to expose the eggs and nestlings. Similar opportunism is displayed by kookaburras and Sacred Kingfishers, which take several species of young and, occasionally, adult birds, as well as mice.

Overall, kingfishers seem to be highly adaptable and will take just about any type of animal prey available. An example of this adaptability was shown by a Malachite Kingfisher, a species which feeds mainly on fish and amphibians. When these prey became unavailable in a polluted river in Kenya, the kingfisher remained in its territory but switched to feeding on water-beetles (Dytiscidae) and water boatmen (Notonectidae) and on adult dragonflies and damselflies. An extreme, and very surprising, instance of adaptability, or perhaps opportunism, involved Pied Kingfishers that were reported scavenging at the carcass of a civet (*Civettictis civetta*).

Plants seem to be the only major type of food that is never regularly used by kingfishers. Even so, there are some reports of the Common Kingfisher diving for pieces of vegetation and eating reed stems, and both it and the Belted Kingfisher occasionally feed on berries. Furthermore, the Blue-breasted Kingfisher feeds on the fruits of the oil palm (*Elaeis guineensis*) in Africa.

In contrast to this diversity of food items taken, the hunting behaviour of the Alcedinidae is fairly uniform. In most species, it consists of sitting quietly on an exposed perch and surveying the surrounding area for prey. When the kingfisher spots something, it swoops down to the ground or dives into the water, seizes the animal in its bill, and returns to the same or another perch.

There are a number of variations on this general pattern. At the end of the swoop, the kingfisher may land briefly on the



Before swallowing ■ large prey item, the kingfisher will beat it several times on the substrate, as is perfectly demonstrated by the Crested Kingfisher. The bird holds the fish by the tail and swings it down so that the head smashes on to the perch, repeating the process a number of times if necessary. This action serves to break the fish's bones and protective spines, which might otherwise stick in the bird's digestive tract. Even so, such mishaps do sometimes occur, often with fatal results for the kingfisher.

[*Megaceryle lugubris lugubris*, Yoroikeikoku (Yoro Ravine), Chiba, Honshu, Japan. Photo: Tsutomu Takahashi]

ground before seizing the prey in its bill. Alternatively, the bird does not land but, instead, snatches the prey item in flight. Sacred, Chattering and Tahiti Kingfishers forage rather in the manner of flycatchers (Muscicapidae). They fly out from a perch to catch insects from foliage, trunks, branches, mudflats or water, sometimes briefly hovering in front of foliage to glean insects from the leaves, or occasionally snapping up insects in flight. Even kingfishers as large as the Blue-winged Kookaburra will occasionally take insects in flight.

The Pied Kingfisher has developed hovering as a means of obtaining food to a greater degree than has any other kingfisher.

This has freed it from the necessity of returning to a perch on the shoreline, and has thus allowed it to exploit new food resources. On Lake Kariba, in southern Africa, it has been observed up to 3 km out from the shore, feeding on the introduced sardine *Limnothrissa miodon*. This fish rises to the surface chiefly at dawn and dusk, and the Pied Kingfisher has adjusted its foraging times accordingly. Fish less than 20 cm in length are swallowed on the wing, whereas larger ones are carried back to a perch and are beaten before being swallowed.

Dives into water can be of two types. Either the kingfisher takes prey from the surface, in which case it does not submerge,



All alcedinids deal with fish prey in the same manner. Once the kingfisher has killed or, at least, stunned its fish, by beating it on a branch or similar substrate, it manoeuvres the prey into a position so that the head is facing backwards towards the bird's gullet. With gulping actions, the kingfisher then swallows the food. This stage-by-stage process is well illustrated here by ■ male Belted Kingfisher, captives of which have been found to have an average daily energy consumption of 55-61 kcal.

[*Megaceryle alcyon*, Cape Cod, south-east Massachusetts, USA. Photos: George J. Sanker/DRK]



Some of the fish taken by kingfishers can appear very big in comparison with the size of the bird itself. The female Amazon Kingfisher, for example, has a bill length averaging about 7 cm, but it catches and consumes fish, especially characids, up to at least 17 cm long. Such relatively big-looking prey, however, rarely present any problem for the kingfisher, which is able to swallow its meal with ease. It is interesting to note here, incidentally, the shed scales of the fish adhering to the bird's lower mandible, something which occurs commonly among the piscivorous members of this family.

[*Chloroceryle amazona*,  
Mamirauá Sustainable  
Development Reserve,  
Amazonas, Brazil.

Photo: Luiz Claudio Marigo]



or it makes deeper plunges and submerges fully, then penetrating a variable depth underwater. As it enters the water in a deep plunge, the Common Kingfisher holds its wings extended back so as to produce a more streamline shape. Once under the water, it covers its eyes with the nictitating membrane, and then uses its own natural buoyancy and a few wingbeats to regain the surface. There are even reports of Common Kingfishers diving through ice to capture fish.

After catching the prey in its bill, the kingfisher returns with the food to its perch, where the animal is beaten before being swallowed head first. Small prey items, such as beetles and other insects, can be dealt with quickly; held in the tip of the bill, the insect is bashed on a branch or on the ground a few times, on alternate sides, this treatment removing its wings and legs, and it is then swallowed. Larger fish are treated more thoroughly. The Common Kingfisher, for instance, will hold a fish by the tail and swing it so that the head smashes down on the perch. Beating fish before swallowing them probably has a vital role in breaking their protective spines and bones, which otherwise could become lodged in the kingfisher's digestive tract. Indeed, there are occasional records of mortality among kingfishers resulting from this problem. One example concerns a dead Common Kingfisher which was found with a bullhead (*Cottus gobio*) wedged in its throat. The fact that freshwater crabs brought to nestling White-throated Kingfishers had their shells already smashed by the parents further illustrates the importance of treating such prey before it is consumed.

Of course, it is not only fish that could be dangerous to the kingfisher. The Blue-winged Kookaburra treats a snake or a snake-like reptile with particular care. It holds its victim near one end, either the head or the tail, and bashes this extremity of the animal several times against the branch, before the reptile is manipulated and mashed in its bill. The kookaburra then tosses its prey so that the other end of the snake protrudes from its bill, and this it again bashes against the branch. This entire process may be repeated several times until, finally, the reptile is tossed so that it lies lengthwise in the bird's bill and can be swallowed head first. In the case of longer lizards or snakes, the tail may protrude from the kookaburra's bill for a long time while the head end is digested.

A less obvious danger faces the Oriental Dwarf-kingfisher. This attractive little alcedinine has been watched extracting large spiders from their webs. The bird flew at the web at great speed, turning at the last moment and attempting to snatch the spider from its home. This is, in fact, a rather dangerous foraging technique, since the lightweight kingfisher occasionally becomes entangled in the web.

Pied Kingfishers avoid conditions of poor visibility, such as turbid or broken water, and generally prefer to fish instead in quiet lagoons, or beyond the breakers on the coast. In calm weather, Pied Kingfishers at Lake Victoria made 80% of dives from perches, but, in unsettled weather, only 14% of dives were from perches while the rest were made from a hovering position. The success of dives from perches was 52%, compared with 41% from hovering. In another study, in South Africa, the success rates from perches and from hovering were 22% and 17%, respectively, while a third study gave an overall success rate of dives of 24% at Lake Victoria and 79% at nearby Lake Naivasha. Clearly, success rate is very variable and will depend on a range of factors, including water conditions and fish density. A Pied Kingfisher has also been recorded taking two fish in one dive, although this success was diminished when one of the fish was dropped at the feeding perch.

On Lake Victoria, there has also been a major change in the prey taken by Pied Kingfishers. Initially, this species' diet consisted mainly of cichlid fish taken inshore, but this supply decreased dramatically with the introduction to the lake of the large, predatory Nile perch (*Lates niloticus*). A small, open-water cyprinid, *Rastrineobola argentea*, also increased in numbers at this time, and Pied Kingfishers switched to this resource, fishing in much deeper water, 1.5-2.5 km offshore, and concentrating their feeding activity in the hours before sunset when the adult cyprinids came to the surface. This fish species now makes up 97% of the diet of the lake's Pied Kingfishers, which, moreover, swallow the fish in the air, in order to avoid the long flights back to the shore.

After considering a range of environmental conditions that might affect where Pied and Malachite Kingfishers concentrated their foraging activities, scientists found that, not surprisingly, it was fish density that was the most important determining param-



eter. For the Belted Kingfisher, water quality is also important in the choice of fishing sites. This large ceryline prefers clear water, together with perches giving an unobstructed view of the water. If the water becomes muddy or turbid after heavy rain, either it will switch from taking fish to taking crayfish or it will, perhaps, leave the area altogether. Belted Kingfishers catch whatever fish are available in their preferred size range and in shal-

low water, but experimental studies have shown that the complexity of the river bottom can affect the availability of different fish species.

A few species of alcedinid forage on the ground, probing and moving aside leaf litter as they search for animal prey. This foraging method is most developed in the Shovel-billed Kingfisher, which uses its extremely broad and deep bill to shovel aside soil and leaves in search of food items. Despite no direct evidence, it is quite possible that the Hook-billed Kingfisher at times forages in a somewhat similar manner, because its bill is frequently caked with soil. Dried earth and insect remains on the lower mandible of a Banded Kingfisher suggest that it, too, had been probing in the ground, and it seems likely that the Rufous-collared Kingfisher may have similar terrestrial foraging behaviour. In addition, the White-throated Kingfisher and the Blue-winged Kookaburra have been seen probing in the ground for earthworms, and Sacred Kingfishers probe into rotten wood, searching for insect larvae.

Some kingfishers exhibit a commensal relationship with other animals, following the latter and catching the smaller animals which they displace. These include the Azure Kingfisher in Australia, which has been observed following foraging platypus (*Ornithorhynchus anatinus*) and snatching the small aquatic animals disturbed by the monotreme's activity on the riverbed. A similar situation has been recorded in Asia, where Stork-billed and Collared Kingfishers have been watched following the progress of smooth-coated otters (*Lutrogale perspicillata*) and feeding on the fish and other aquatic animals disturbed by the otters. The Pied Kingfisher has also been recorded hovering above and following a foraging Long-tailed Cormorant (*Phalacrocorax africanus*) and a clawless otter (*Aonyx capensis*), catching fish displaced by the other animal, as well as using a hippopotamus (*Hippopotamus amphibius*) as a perch. In the forests of central Africa, the Chocolate-backed Kingfisher has been seen to accompany columns of driver ants, feeding either on the ants themselves or on insects which they flush. White-throated Kingfishers closely follow grazing cattle to snatch the insects which they disturb, and Belted Kingfishers hover above foraging egrets (*Egretta*) to catch some of the displaced fish. Blue-winged Kooka-



Clearly, some kingfishers are capable of catching more than one fish at a time. This Crested Kingfisher has succeeded in capturing two reasonably sized fish; the fact that both are still alive indicates that they were taken in a single dive. Although multiple catches are an infrequently observed phenomenon, they probably occur regularly when hunting conditions are favourable, and have obvious benefits in terms of the individual bird's energy expenditure.

[*Megaceryle lugubris lugubris*, Yoroikeikoku (Yoro Ravine), Chiba, Honshu, Japan. Photo: Tsutomu Takahashi]

The Stork-billed Kingfisher is one of many alcedinids that include crustaceans in their diet. This large species, as well as its two equally big congeners, has a deep-based bill that is very long in relation to the bird's body size, and this would seem to be a particularly useful tool for dealing with such hard-shelled items as crabs and crayfish, which represent a large proportion of the food taken by this kingfisher. All the same, it does consume a large number of fish, too.

[*Pelargopsis capensis javana*, Ujung Kulon National Park, west Java. Photo: Alain Compost/Bruce Coleman]





Most kingfishers that live in woodland and forest feed on invertebrates. Grasshoppers and other orthopterans, along with a wide variety of other insects, frequently feature prominently in the diet of many alcedinids, from the largest ones right down to the tiny species in the genus *Ceyx*. The African Pygmy-kingfisher, for instance, catches large numbers of orthopterans, lepidopterans, flies and beetles, as well as other arthropods and some small vertebrates. This individual was returning to its nest in the side of an aardvark (*Orycteropus afer*) burrow when it conveniently paused on a favourite perch. In its bill it is carrying a locust. That this is destined as food for one of the four chicks known to be in the nest at that time can be surmised by the fact that the insect is being held with its head facing away from the kingfisher. Had the adult been intending to eat the locust itself, it would have held the prey the other way around, so that it could be swallowed head first.

[*Ceyx pictus natalensis*,  
Langjan Nature Reserve,  
Northern Province,  
South Africa.  
Photo: Geoff McIlleron]



In the arid or semi-arid habitats in which it lives in Australia, the Red-backed Kingfisher exhibits a high degree of opportunism in its feeding behaviour. This is another alcedinid that eats a great variety of insects, again with orthopterans often predominating, but phasmids and mantids are also common prey. In addition, it takes vertebrates ranging from fish and amphibians to reptiles and small mammals. A pair of Red-backed Kingfishers has even been known to peck at the mud nests of Fairy Martins (*Hirundo ariel*) until the tunnels broke away, allowing the kingfishers access to the eggs and nestlings.

[*Todiramphus pyrrhopygius*,  
Australia.

Photo: J. J. Brooks/Aquila]

burras often follow the front of bush fires, where they seize the animals fleeing from the fire.

In some cases, the feeding association with other animals is not a commensal one but, rather, an example of piracy. Sacred Kingfishers have been recorded stealing earthworms from Black-birds (*Turdus merula*) and Song Thrushes (*T. philomelos*), two species which were introduced into New Zealand, and Common Kingfishers have been reported harassing and robbing water shrews (*Neomys fodiens*) and robbing White-throated Dippers (*Cinclus cinclus*) of fish. Even more amazingly, there are reports of Laughing Kookaburras stealing a snake from a hawk and a frog from the mouth of a green tree-snake (*Dendrelaphis punctulatus*).

Some interesting mysteries remain concerning the feeding methods of kingfishers. Scorpions, up to 90 mm long, have been recorded in the stomach contents of the Rufous-collared Kingfisher, but there has been no sign of these arachnids' stings. How the dangerous stings were removed is yet to be discovered. Although direct observations are lacking, circumstantial evidence exists that Ruddy Kingfishers use stones on the forest floor as "anvils", to enable them to crack open the shells of large land snails.

## Breeding

Some aspects of the breeding biology of the kingfishers are common to all members of the family. All alcedinids have similar nest-sites, in the form of a chamber at the end of a tunnel in a bank, a tree or a termite nest, and all have similar white eggs. In many other respects, however, their breeding activities reveal great differences among the species. Only a handful of kingfishers have been studied in detail, but these have provided a wealth of comparative information.

All kingfishers establish territories of varying size. Male Belted Kingfishers hold territories along rivers or on lakes, and these are defended by aerial chases and loud rattle calls. Females visit these territories and, once paired, both sexes will defend the territory against conspecifics. Other avian species are tolerated in the territory, but raptors are sometimes mobbed.

Common Kingfishers are very strong in the defence of their territories. Initial interactions take place, with two birds perched about a metre apart, sitting upright, with the bill partly open and swept from side to side while the kingfisher watches its rival. In a higher-intensity forward-threat display, the bird turns sideways on, bows forward until it is lying with the neck extended along the perch, and sways from side to side or makes jerking movements. This is often followed by a flying attack at a perched bird, by the two bill-grappling, or by an aerial chase. The two may topple into the water and continue to fight there, trying to duck each other under the water. Most of these aggressive encounters are short in duration, but one continued for over eight hours. In some cases, the kingfisher enters a neighbour's nest-hole and punctures the eggs.

When establishing a territory, a Forest Kingfisher may fly at a rival on a perch, making contact, and with the two birds locking bills. They then fall, spinning, while still locked together. After landing on the ground, they break free and fly off to separate perches.

At the start of the breeding season, the male White-throated Kingfisher delivers its song for long periods, mainly in the early morning, from an exposed perch or, rarely, from the ground. It sits with its tail turned under the perch, periodically flicking its wings open in a vertical plane to expose the white wing patches. In courtship, the male cocks its tail and droops its wings, again exposing the white patches. It also performs aerial displays with loud calling and screaming, the kingfisher sometimes ascending 50-60 m in the air and then diving in a tight spiral to below the treetops. The female invites copulation with a distinctive call and shivers her partly open wings. African *Halcyon* kingfishers also have very distinctive displays with outspread wings, similarly showing off the inner white patches, all such behaviour being accompanied by much calling.

Pair formation by the Common Kingfisher begins with aerial chases in association with the giving of the advertising call from several perches. The female watches while the male starts nest-digging, and the male may fly to and from her several times. Both sexes sometimes share the digging of the first tunnel, but it is chiefly the male that digs the second. Courtship feeding starts





While the habits of most of the paradise-kingfishers in the genus *Tanysiptera* are poorly known, the information available indicates that these attractive species are primarily insectivorous, rarely, if ever, taking any fish. The best-studied of the group is the Buff-breasted Paradise-kingfisher, which is known to feed on a wide variety of invertebrates, including phasmids, but ranging from beetles and grasshoppers to mantises, cicadas and even bees and wasps. It also eats snails, and supplements its diet with some vertebrates, among them frogs, tortoises and lizards. In addition, this alcedinid consumes earthworms, which it presumably obtains by digging in soil, and various other prey are also taken on the ground. Observations suggest, however, that most of its food is snatched from foliage in a technique referred to as sally-hovering.

[*Tanysiptera sylvia sylvia*,  
Mount Spec,  
near Townsville,  
Queensland,  
north-east Australia.  
Photo: C. & D. Frith]



A typical example of a woodland-dwelling alcedinid is the Grey-headed Kingfisher, a reasonably common species throughout much of the Afrotropics. This kingfisher, like others which live in similar habitats, is primarily an insectivore. Although it does include in its diet a few reptiles and occasionally other vertebrates, by far the highest percentage of its food is made up of such insects as grasshoppers, locusts and crickets, cockroaches, mantises, ants and Lepidoptera; some spiders and small scorpions are also caught. Caterpillars are a frequently taken item, and are commonly fed to the young. The individual shown in this photograph was nesting in the roof of an underground mammal burrow; before entering to feed a juicy green caterpillar to its young, it perched briefly on a nearby branch.

[*Halcyon leucocephala pallidiventris*, near the Zimbabwe Ruins, close to Fort Victoria, Zimbabwe.  
Photo: Cyril Laubscher]



Even the biggest of kingfishers eat small prey, as well as larger ones. Although the Blue-winged Kookaburra is capable of killing and eating animals up to the size of reptiles and small birds, it will not miss the opportunity to catch any suitable item that it comes across, whether vertebrate or invertebrate. Observations of the prey taken by this species at Kakadu, in north Australia, indicated that 59% of items were invertebrates and 41% were vertebrates.

[*Dacelo leachii leachii*,  
Kakadu National Park,  
Northern Territory,  
Australia.  
Photo: Hanne & Jens  
Eriksen]



when the nest is almost complete, and often follows a chase. The male presents his mate with a fish, this being accompanied by contact calls, and with the female sometimes shivering her wings or giving a begging call. Courtship feeding declines rapidly in frequency with the onset of incubation.

Courtship feeding is sometimes used to establish the pair-bond. After a male Belted Kingfisher catches a fish and returns with it in his bill to the perch, a female will land nearby and the two will approach each other, making 180° turns, until they are side by side. The female is then given the fish, which is swallowed immediately. Courtship feeding is important in the breeding behaviour of the Pied Kingfisher, starting at the time of nest excavation and terminating when the eggs hatch. The female of that species solicits food with a begging call and adopts a begging posture. The male, meanwhile, holds the fish so that its head is nearest the bill tip and, after a brief struggle, the food item is transferred to the female. The female then pecks at her mate, and he departs.

With the Buff-breasted Paradise-kingfisher, courtship involves the male chasing the female in wide circles around potential nest-sites. These chases are sometimes interrupted briefly, as the birds sit on the nest mound, normally a termitarium, and call to each other. They are very aggressive towards conspecifics and also other species, including Noisy Pittas (*Pitta versicolor*), Eastern Whipbirds (*Psophodes olivaceus*) and Emerald Doves (*Chalcophaps indica*), driving them away from the nest-site.

Nesting pairs of Common Kingfishers are usually well spaced, generally 1-2 km apart on the river, with neighbours only rarely coming as close as 125 m to each other. Non-breeding territories of the Belted Kingfisher are half the size of breeding territories in Ohio. The location of a suitable nest-site is the proximal factor in determining the position of a territory, but the size of the territory is then determined by the need for adequate food resources.

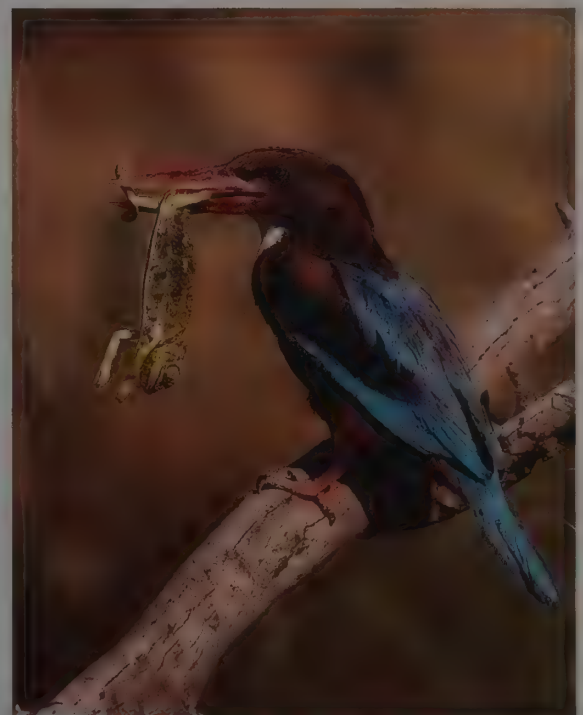
Pied Kingfishers will breed singly, and defend linear territories, along rivers where food and nest-sites are plentiful. Where breeding sites are scarce, however, they nest in colonies of twelve to 100 or more birds. Within the colony, the distance between individual nesting tunnels can vary between 0.5 m and 5.2 m, and adults defend only the area in the immediate vicinity of the nest-hole. The Ringed Kingfisher is also generally a solitary

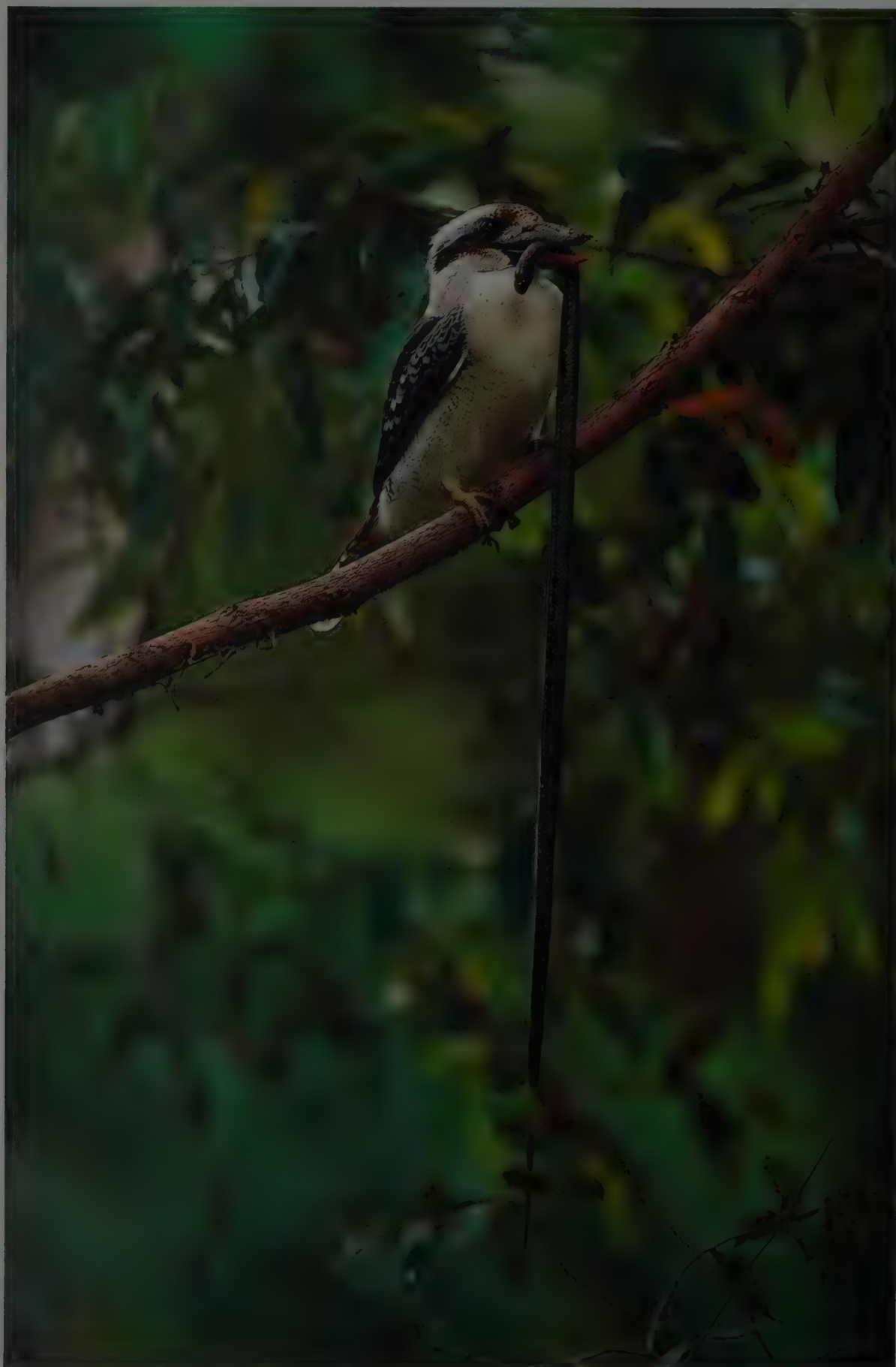
breeder, although colonies of four or five pairs are reported from the Orinoco River, in Venezuela, and there is an exceptional early record of 150 pairs breeding together in a colony.

While the majority of kingfishers are monogamous, with a single pair responsible for breeding activities, there are a number of alcedinid species which are communal breeders, the pair having a variable number of helpers to assist with its reproductive activities. Observations at a series of lakes in Kenya suggest that the reproductive behaviour of the Pied Kingfisher is determined by fish availability. Where fish density is very low, Pied Kingfishers do not breed or they leave the area, as occurred at Lake

Lizards and chameleons are a frequent item on the menu of the White-throated Kingfisher, a common and conspicuous bird throughout its south Asian range. The food spectrum of this species is extremely broad, ranging from numerous types of invertebrate to amphibians, reptiles, birds, small mammals and fish. With such a wide choice available, it is interesting that some individuals or populations of this kingfisher specialize on certain types of prey, and avoid others that are equally accessible to them.

[*Halcyon smyrnensis smyrnensis*,  
Israel.  
Photo: Yossi Eshbol/  
FLPA]





Although a number of alcedinids capture and eat snakes, it is the two big kookaburras of Australia that are justly renowned for their ability to overcome these potentially dangerous reptiles. The diets of both species have been well studied, and snakes feature prominently among the many different foods eaten. The Laughing Kookaburra is able to kill snakes up to 1 m in length. It takes a firm grasp of the reptile just behind the head, and then bashes it violently on the ground, or on a suitable perch, to immobilize it. Sometimes it stuns large snakes by carrying them into the air and dropping them from height. The kookaburra finally swallows its victim head first, but it may be some time before the head end is properly digested, so that the tail may droop from the resting bird's bill for quite a while. This familiar and fearless kingfisher has also been recorded as stealing a snake from a raptor, and even robbing a snake itself of its intended meal. At the other extreme, it will often visit bird-feeding tables and picnic areas, where it accepts scraps of food, and in some areas it frequents refuse tips to take advantage of the easy pickings available there in the form of household waste.

[*Dacelo novaeguineae*  
novaeguineae,  
south Queensland,  
Australia.  
Photo: Glen Threlfo/  
Auscape]



Courtship feeding is used in several different contexts during the earlier stages of the breeding cycle. It sometimes features as part of the ritual in establishing the pair-bond, when the female lands near a food-carrying male and the two approach each other with a certain caution, until close enough for the male to present the meal to his intended mate. This seems to be the case with the two Ruddy Kingfishers shown here. Courtship feeding occurs most often, however, during the nest-building and pre-laying phases, and the female may then solicit food from her partner by adopting a begging posture.

[*Halcyon coromanda major*,  
Chitose River,  
Hokkaido, Japan.  
Photo: Tadashi Shimada/  
Oasis]



Nakuru and Lake Baringo. With higher density of fish, breeding is attempted, but with low success rates unless assisted by helpers, as demonstrated at Lake Victoria. When fish are plentiful and in high density, breeding is successful even without the aid of helpers.

Common Kingfishers are chiefly monogamous, and members of a pair can breed together for more than one season, but changes of mate during the season are also not uncommon. The partners usually share the nesting activities. When second and third broods overlap, as not infrequently occurs with this species, the male may do nearly all of the brooding and feeding of the second brood while the female lays and incubates the third, but in some cases the male incubates while the female broods and feeds the existing young. In one instance, when the female died four days before hatching, the single male hatched the eggs and successfully reared the young alone. One male breeding with two or, rarely, three females is recorded in up to 35% of nestings in Russia. In these cases of polygamy, the male is able to partake in the incubation and rearing of six broods in one season.

In north-east Australia, a female Buff-breasted Paradise-kingfisher successfully bred at the same site near Mackay, in Queensland, for three successive years, each time with a different male. In the fourth year, she initially started nest-tunnelling with a new male but, after about ten days, her mate from the previous year arrived, drove off the new male, and the pair bred successfully in a new nest. The Belted Kingfisher is generally a monogamous species, but there is one record of a juvenile bird feeding the young of a different brood. A territory of White-throated Kingfishers sometimes holds three adults, suggesting the possibility of communal breeding, but this is yet to be confirmed.

Communal breeding by Pied Kingfishers breeding on Lake Naivasha and Lake Victoria, in East Africa, has been thoroughly studied. This species has a biased sex ratio among adults of 1.8 males to 1 female, but an even sex ratio among the young. This unequal adult sex ratio probably results from young females exhibiting a greater degree of dispersal away from the nest-sites and, later, undertaking a greater proportion of the incubation and brooding activities than do the males, which results in higher mortality among females. The helpers of Pied Kingfisher pairs are invariably males, and they are either primary helpers, being one-year-old sons of the nesting pair, or secondary help-

ers, which are unrelated to the nesting pair and are either surplus males or males which had failed in their own breeding attempts. Primary helpers provide assistance from the start of nesting, by bringing food to the breeding pair; subsequently, they help to defend the nest-site from rival kingfishers and from predators, and later bring food to the nestlings. Secondary helpers bring food to the colony and try to feed females before egg-laying. The resident males drive them off until a few days after the eggs hatch, at which time these helpers fly through the colony with a fish in the bill and try to feed brooding females in the nest-tunnels. Initially, they are repelled by the male of the pair, but, if they persist for several days, they may be accepted, after which they continue to feed the young and defend the nest against predators. It was found that Pied Kingfisher pairs were more likely to accept helpers in areas where resources were scarce than they were in those areas with more plentiful fish. Thus, at Lake Victoria, with fewer fish, 66% of pairs had helpers, whereas at Lake Naivasha, where the food supply was much better, only 28% of pairs had helpers. Furthermore, at Lake Victoria, those pairs with helpers had significantly better breeding success than did those without. For pairs with one helper, 78% of hatched birds fledged, and the corresponding figure for those with two helpers was 100%; this compares with a success rate for unhelped pairs of only 39% of hatched birds fledging. Secondary helpers often return to breed in the area where they had helped in the preceding year, sometimes pairing with the same female as they had previously helped.

The Laughing Kookaburra is a co-operative breeder, with helpers assisting the breeding pair in incubating the eggs, and brooding and feeding the chicks and fledglings. Studies at Canberra, in south-east Australia, have shown that the helpers are usually the offspring of the breeding pair and that both sons and daughters help, although the daughters usually disperse earlier than do the sons. The latter are much better helpers than are daughters, but their contribution becomes less as the size of the group increases. One helper makes a small improvement to the productivity of the breeding pair, but large groups of seven or more birds perform worse than does a single pair. The members of a breeding pair are very faithful to each other and remain together for many years, probably until one of them dies. In some bird species, helpers may also "cheat", with male helpers sneak-



A further example of courtship feeding, which is rather frequent among the Alcedinidae and is likely to be part of the behaviour of all species in the family, is provided by the Crested Kingfisher. This striking species, which ranges from Afghanistan and the Himalayas east to South-east Asia and Japan, is probably fairly typical in this aspect of its breeding behaviour. A male is here presenting a fish to his mate. It is interesting to reflect that the posture adopted by the female is closely similar to that used by the young kingfishers when begging for food. Courtship feeding may be primarily a symbolic type of behaviour, rather than ■ means of satisfying any increased dietary requirements of the female. Since kingfishers are highly territorial and generally rather aggressive birds, it probably serves initially to reduce aggression between the two partners, and at the same time to give an indication of the male's ability to provide enough food for a future family to be reared successfully. Subsequently, its function is probably to strengthen and maintain the pair-bond. In most alcedinids for which relevant information is available, courtship feeding is far less regular, or may cease altogether, once incubation has started. This would seem to support the idea that it is principally symbolic in nature.



[*Megaceryle lugubris*  
*lugubris*,  
Yoroikeikoku (Yoro Ravine),  
Chiba, Honshu, Japan.  
Photo: Tsutomu Takahashi]



Copulation has been well documented for a number of alcedinids, among them the widespread Common Kingfisher. This is one of several species in which copulation is preceded by courtship feeding.

The male then hovers briefly over the female's back, and she leans forward until almost horizontal. He mounts her and grasps her nape feathers in the bill, while flapping his wings to maintain balance; as the female moves her tail sideways, cloacal contact takes place briefly. The male immediately flies off, often to bathe.

[*Alcedo atthis ispida*, near Munich, Bavaria, Germany.  
Photo: Günter Ziesler]



ing copulations with the breeding female, or female helpers laying their eggs in the nest, but these events are very rare in occurrence in the Laughing Kookaburra.

Two-thirds of breeding pairs of the Blue-winged Kookaburra also have one or more auxiliaries, and 85% of these auxiliaries are males. These helpers assist with most of the breeding activities, including the preparation of the nest, the feeding of the breeding female prior to laying, the incubation and feeding of the chicks, and territorial defence.

For both the Chattering and the Striped Kingfishers there are reports of birds living as trios consisting of two males and one female, and with both of the males mating with the female. These reports are in need of further investigation, in order to reveal more details of the relationships among the three adults.

Most kingfishers nest in earth banks, either naturally formed ones at the sides of rivers and lakes, or artificial ones formed by the construction of banks, roadside ditches, or sand and gravel pits. Some species use tree holes, and a few burrow into the trapped soil around the roots of a large tree which has fallen over. Many forest kingfishers use the arboreal nests of termites. The Common Kingfisher occasionally nests in the burrow of a rabbit (*Oryctolagus cuniculus*), and the Malachite Kingfisher sometimes breeds in an aardvark (*Orycteropus afer*) burrow. A Ruddy Kingfisher was once recorded making a nest-chamber in a nest of hornets.

There are no confirmed reports of kingfishers ever using anything but a tunnel for a nest. Although a White-throated Kingfisher in Assam, in north-east India, was said to have utilized an oval structure of moss wedged into a hollow, this has never been reported subsequently and requires substantiation. The Beach Kingfisher nests in tree holes, but it is also suspected of nesting occasionally in the fibrous material in the heads of coconut palms. A pair of Forest Kingfishers once excavated a nest in a clump of staghorn fern (*Polypodium*).

Belted Kingfishers usually nest in earth banks near water, although a range of other structures can be used. These include ditches, road cuttings, sandpits or gravel pits, piles of sawdust or mud, furrows in a ploughed field and tree holes. The nest-site is chosen during courtship, with the male flying to the bank and slashing and probing there with his bill, while the female calls from a nearby perch. Both sexes excavate the burrow, although the male spends twice as much time digging as does the female. One bird usually digs for periods of one to two minutes, using its

feet to eject a plume of soil from the entrance. Its mate sits nearby and calls continuously. Most digging is done in the early morning, although the pair may return again in the early evening. The majority of nests are excavated within three to seven days, but heavy rain can cause a delay of several days. Large rocks or tree roots in the way of a tunnel can cause the route of the tunnel to bend, or the nest may have to be aborted. Clay or gravel banks are generally unsuitable for nest-sites. The tunnel entrance is usually high up in the bank, 30-60 cm below the top, a situation which will serve to reduce predation and flooding. The tunnel has an average length of 1 m and often inclines upwards, which again will reduce the risk of flooding. It ends in a nest-chamber 20-30 cm in diameter and 15-17 cm high. The nest is unlined, but a layer of broken-down pellets starts to accumulate on the floor during the incubation period.

In contrast to the Belted Kingfisher, Buff-breasted Paradise-kingfishers excavate their nests in termite mounds, either on the ground or in trees. The termitaria are often occupied by living termites, and these reseal the tunnel and nest-chamber at the end of each season, so that it needs to be excavated anew each year. The same mound can be used for at least three years in succession. Both sexes excavate the nest. While one is digging, the other perches nearby, seemingly on guard, and calling softly. As the kingfisher digs into the mound, loose earth is pushed out by the birds's body or, if it is able to turn around, scooped out in the lower mandible. Female paradise-kingfishers also use the long tail to sweep out loose soil as they dig, but, interestingly, the male holds his tail up while digging.

Several species of kingfisher dig their nest-holes by flying at the chosen site and hitting it with the bill to dislodge the earth or wood. The initial hits are made with considerable force, the bird often bouncing off and, sometimes, becoming fatally injured. As the earth becomes looser, the birds perch at the site and probe with the bill to remove the material. A pair of Stork-billed Kingfishers spent several weeks trying to dig a hole into a brick wall. Although that attempt was doomed to failure, another species, the Ruddy Kingfisher, has successfully excavated tunnels in the mud walls of village huts.

The Common Kingfisher often rears more than one brood in a season. The male often starts to dig a new nest-tunnel before the first brood has fledged, but the pair may revert to using the original nest for a third brood. This species reuses its nests in successive years. Pied Kingfishers vary in their reuse of nest-





All kingfishers nest in a chamber at the end of a tunnel, which may be excavated in a bank or in a termite nest, or in a hole in a tree. In the case of the Yellow-billed Kingfisher, for example, the pair usually digs its nest in an active arboreal termitarium of *Eutermes* species, but occasionally in a tree hollow, and the site can be up to 15 m above ground, although it is normally somewhat lower. One nest of this kingfisher had an entrance 4 cm wide and 4 cm long, leading to a chamber that was over twice that size in height and breadth and was 12 cm deep.

[*Syma torotoro flavirostris*, Nesbit River, Iron Range area, Cape York Peninsula, north Queensland, Australia.  
Photo: C. & D. Frith]

sites. In some places they use the same tunnel year after year, but in others they dig a new tunnel each year, even if the previous one is intact. If the pair-members separate in the non-breeding season, the male subsequently returns to the previous nest-site, while the female moves elsewhere.

The nesting tunnel can vary in length according to its location. For example, that of the Oriental Dwarf-kingfisher is up to 1 m long when located in a streambank or a cutting, and one pair took only 40 minutes to dig 25 cm in sand. When that species' nest is located in a ground termitarium or in the soil collected between the roots of a fallen tree, however, the tunnel is of necessity considerably shorter. For Blyth's Kingfisher (*Alcedo hercules*), a nest-tunnel in sandy ground was reportedly 2 m long, but in harder ground the tunnels were 40-60 cm in length. As with most other alcedinids, its tunnels are generally horizontal or incline slightly upwards, probably to prevent water running down to the nest-chamber. The Crested Kingfisher excavates a nest-tunnel 2-3 m long, but the record for length is held by the Giant Kingfisher, with a tunnel measured at 8.5 m.

The nest-chamber has no lining but, once the eggs hatch, the floor becomes covered in a mass of faeces and discarded food remains. Nestlings of the Belted Kingfisher forcefully void their liquid excreta against the wall of the chamber; they then turn around and, using the bill, hammer the earth above that part of the wall, so that the excreta are buried. The nest-chambers of Pied Kingfishers become wider and lower with time as the nestlings dig out the soil from the walls, an action which helps with sanitation in the nest. No similar behaviour appears to be conducted by the young of the Buff-breasted Paradise-kingfisher, the nests of which become foul with faeces and food remains, and are often infested with the larvae of tachinid flies. In some nests, the young defecate out of the tunnel when they are twelve to 15 days old, leaving a visible white line of faeces up to 60 cm from the entrance. Before brooding at night, the female cleans out the nest-chamber, removing items of uneaten food. Nestlings of the White-throated Kingfisher defecate towards the nest tunnel, thereby keeping the chamber clean, but not the tunnel. A similar situation applies with the Red-backed Kingfisher, where ants may help to keep the nest clean by carrying off excreta and organic matter.

The timing of breeding by alcedinids varies considerably, depending largely upon the latitude of the population being considered. At subtropical and temperate latitudes, the breeding sea-

son coincides with the spring and summer months. The laying season of the Common Kingfisher, for example, is from January to June in Malaysia; in Britain, however, it occurs in March to July, but mainly in April, while in Sweden this species lays primarily in May. The Belted Kingfisher begins nest-building in April in the southern USA, but this work continues until as late as June in the north. The Pied Kingfisher breeds in spring and summer at higher latitudes, in winter in the northern and southern tropics, and throughout the year in equatorial latitudes.

The breeding season of Malachite Kingfishers at Lake Nakuru, in Kenya, coincided with the periods of highest fish density, and that of the Pied Kingfishers at St Lucia, in eastern Natal in South Africa, coincided with periods of low wind velocities and low water turbidity, factors which would facilitate fishing success. In Australia, the onset of breeding by the Yellow-billed Kingfisher in tropical Queensland may be dependent on the start of the summer rains; observers found that, on the day immediately after heavy rain, nest-digging commenced.

Copulation has been observed for a number of kingfisher species. In the case of the Belted Kingfisher, it sometimes follows courtship feeding. The male mounts the female, and flutters his wings to balance while treading on her back; the female cocks her tail to one side and cloacal contact follows, lasting seven to twelve seconds. After copulation, the pair often gives an aerial display, with the female following the male as he soars high and then dips close to the river or lake. After the female returns to a perch, the male continues to spiral high in the sky, stalling at the top and then somersaulting down, before pulling out into an upward glide, with wings fully extended to show the white inner vanes of the flight-feathers.

In the Common Kingfisher, too, copulation is usually preceded by courtship feeding, following which the male briefly hovers over the female's back. The female leans forward almost horizontally, and her mate then lands on her back, holding her nape in the bill and flapping his wings for balance. The female moves her tail sideways for brief cloacal contact, after which the male flies off and, often, bathes. For eight days prior to the laying of the first clutch, a high frequency of copulation is maintained, with four matings recorded in a period of three hours, but the level is reduced for the second clutch.

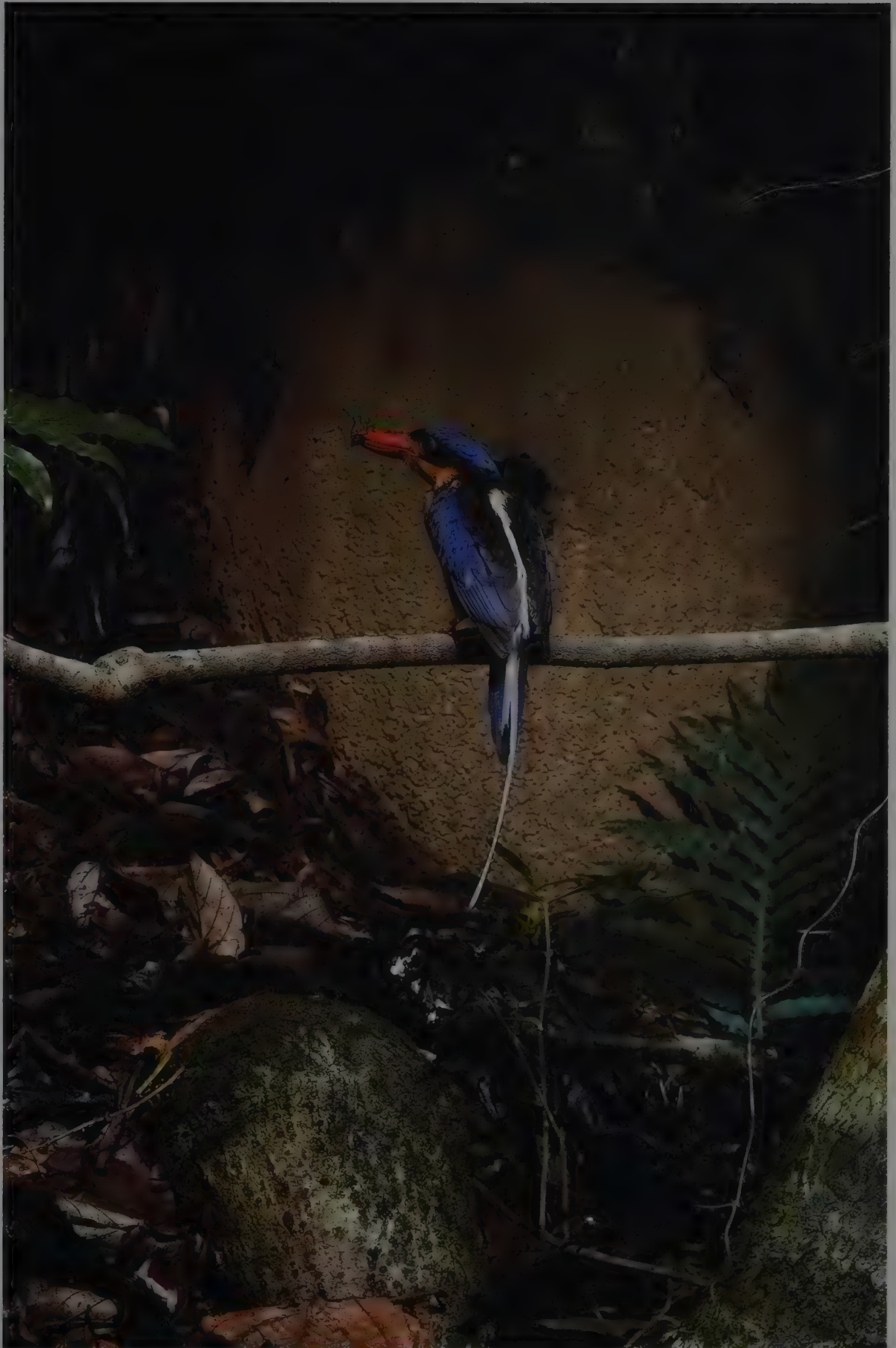
The Laughing Kookaburra copulates in the normal manner, with the male hopping on to the female's back, holding her nape



The paradise-kingfishers inhabiting the dense tropical forest of New Guinea and north-east Australia are typical of those alcedinids which exploit termite nests for breeding. All of the eight species for which the breeding behaviour is sufficiently well known nest in termitaria. One of the better-studied members of this group is the Buff-breasted Paradise-kingfisher, an adult of which is here perched outside its completed nest; as it is holding an insect in its bill, presumably to be fed to its young, the breeding cycle is already well advanced.

This species usually excavates into a termitarium situated on the ground, but will also on occasion use an arboreal one. Each sex works in turn while the other sits nearby, apparently on guard. It is interesting to note that, during the digging process, the female sweeps out loosened material with her elongated central tail feathers; the male, on the other hand, seems never to do this, but instead he holds his tail up and out of the way. There are records of Buff-breasted Paradise-kingfishers using the same nest-site repeatedly for several years in succession; since the termites repair the damage, however, and reseal the tunnel and chamber after the kingfishers have completed their breeding activities, the birds have to excavate a new nest every season.

[*Tanysiptera sylvia sylvia*,  
Mount Spec, Paluma,  
near Townsville,  
Queensland, Australia.  
Photo: C. & D. Frith]





All kingfishers lay smooth, slightly glossy, white eggs that are broadly elliptical to spherical in shape, but clutch sizes vary considerably. While three to six eggs is about the average for the majority of species, the Common Kingfisher generally lays six or seven eggs, and up to ten have been recorded. The laying interval is one day, and incubation generally begins with the last egg, so that hatching is synchronous. With few exceptions, this pattern appears to be the norm for the family.

[*Alcedo atthis ispida*, Rio Adaja, Ávila, Spain. Photo: José Luis Rodríguez/Nature & Travel]

with his bill, and wing-flapping for balance. Copulation takes up to 25 seconds, but is often shorter. There are, however, cases when the female has been seen to mount the male, and attempted copulation between two males, and between the breeding female and an auxiliary, her son, have also been recorded among Laughing Kookaburras.

The eggs of kingfishers are invariably white in colour, and are smooth and slightly glossy. The shape varies from spherical to broadly elliptical. Clutch size varies considerably. Many species, ranging from the small Variable Dwarf-kingfisher and White-bellied Kingfisher to the much larger Hook-billed Kingfisher and Rufous-bellied Kookaburra, have a full clutch of two eggs. At the other extreme, the Common Kingfisher lays up to ten eggs, but six or seven is the normal number. Most species, however, have clutches of between three and six eggs. That of the Belted Kingfisher is normally six or seven eggs, and rare reports of eleven or 14 may be the result of two females laying in the same nest. Clutches of the Belted Kingfisher are equivalent to 37-52% of the female's body weight.

Belted Kingfishers begin egg-laying up to a week after the nest is complete, the eggs being laid in the early morning on consecutive days. Apart from when laying an egg, the female seldom visits the nest until incubation commences. The eggs usually hatch synchronously, over a period of twelve to 18 hours, starting before dawn. Similarly, the Common Kingfisher lays one egg each day and incubation starts with the last egg, so that, again, hatching is synchronous. The Buff-breasted Paradise-kingfisher and the Pied Kingfisher also lay one egg daily, and a laying interval of one day appears to be the rule in this family. In the Pied Kingfisher, however, incubation starts with the first egg, so that hatching is asynchronous, extending over about three days.

The Laughing Kookaburra also starts incubation before the usual clutch of three eggs is complete, which again means that the eggs hatch at intervals. The kookaburra chicks are naked and blind at hatching, and at this early stage of their development they have a sharp hook at the end of the upper mandible, which they use to bite and kill their siblings. The youngest chick suffers most from these attacks. In about half the nests studied at Canberra, the youngest of the brood died within the first week;

in some cases, the eldest would also kill the second-hatched chick. If food is scarce and the start of incubation is delayed, so that the first and second chicks hatch close together, then it is almost certain that the third chick will be killed, as the two older ones contest the top position and direct a great deal of aggression at the smallest chick. If incubation starts earlier, however, so that the first and second chicks hatch a day apart, then the dominance hierarchy is more quickly established and the smallest chick has more chance of survival.

With a process that is not understood, Laughing Kookaburras are also able to manipulate the sex of their hatchlings. Detailed studies found that over 75% of first chicks were males; second chicks were most likely to be females, the proportion being 87% in broods raised by pairs without helpers, while the third chicks showed no bias towards being either male or female. At the time of fledging, the sex ratio is equal. These disparities can be explained as strategies for achieving maximum productivity. Males are physically smaller than females. So, even though the first-hatched chick will obtain the greatest share of food brought to the nest, nevertheless, if it is a male, there will be more food left over to feed the younger chicks; the latter are therefore more likely to survive any food shortages after the initial period of intense siblicide. When the second chick is a female, her larger size and faster growth rate mean that there is soon little difference in size between the first, male, chick and herself, and the high level of aggression between the two increases the chances of the third chick dying. This early siblicide may seem wasteful but, if resources are scarce, it is more efficient for the brood size to be reduced early, rather than for a chick to be fed for several weeks only to die later of starvation.

Incubation periods are known for only a small number of kingfishers. They range from about two weeks to four weeks, depending on species. The documented periods are 13-14 days for the Woodland Kingfisher, 17-18 days for the Sacred, Forest and Grey-headed Kingfishers, 19-21 days for the Common Kingfisher, 20-22 days for the Azure Kingfisher, 22 days for both the Amazon and the Ringed Kingfishers, 20-23 days for the Red-backed Kingfisher, 23-24 days for the Belted Kingfisher, and 23-26 days for the Laughing and Blue-winged Kookaburras. The



A Belted Kingfisher brings food to its nest, typically sited in a well-drained, bare vertical bank near water. The young of this species are brooded almost continuously, mainly by the female, until they are four days old. During this period, the male provides almost all of the food, and he continues to be the main supplier throughout the nestling period. The adults regurgitate the food for the chicks in the early stages, but later they bring in one fish at a time in the bill, this meal then being eaten by a single nestling.

[*Megaceryle alcyon*,  
Ohio River,  
south-west Ohio, USA.  
Photo: Maslowski Photo]



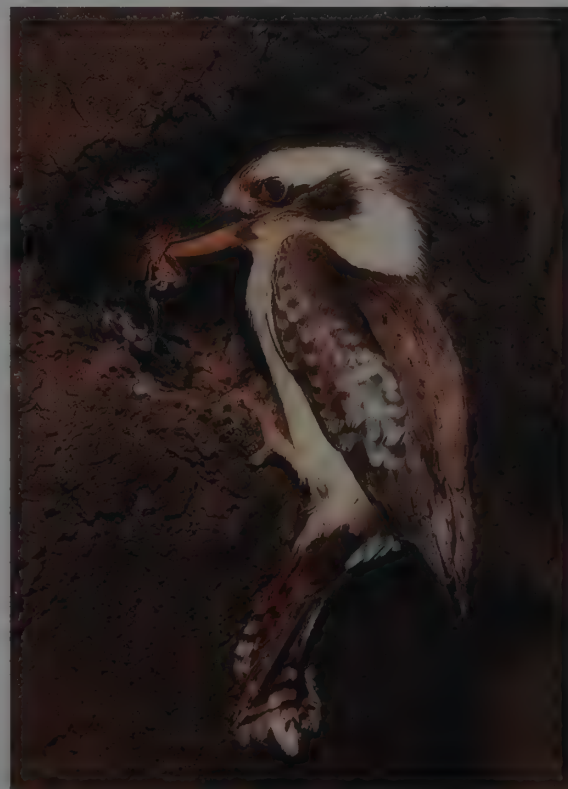
longest incubation period recorded is 26-28 days, for the Buff-breasted Paradise-kingfisher.

Generally, both sexes incubate, but with some clear temporal differences. The female Pied Kingfisher, for example, incubates exclusively at night and for the greater part of the day, accounting for 70% of the total incubation time. In the case of the Belted Kingfisher, the female stays in the nest-burrow overnight and her mate relieves her in the early morning. With the Common Kingfisher, either the two sexes take equal turns, or the male incubates in the afternoon and the female sits overnight and in the morning. Both sexes of the Buff-breasted Paradise-kingfisher incubate during the day, but only the female does so at night, and at one site the female alone brooded, although both parents brought food to the young.

As with incubation, information on nestling periods has been documented for only a few species. Periods range from 21-28 days for the Azure Kingfisher, 22-24 days for the Woodland Kingfisher, 23-27 days for the Common Kingfisher, and 26-31 days for the Buff-breasted Paradise-kingfisher, the Forest, Collared, Sacred, Red-backed and Green Kingfishers and the American Pygmy-kingfisher, to 32-44 days for the largest alcedinids, such as the Crested, Giant, Ringed and Belted Kingfishers and the Laughing and Blue-winged Kookaburras.

During incubation, the female Belted Kingfisher folds her wings over the back. At hatching, however, she lowers them to the ground and stands over the eggs and young. The young of this species are brooded, mainly by the female, almost continuously for the first four days, but brooding ceases after six days. For the first three or four days, the adults carry fish back to the nest in the oesophagus; in the nest-chamber, several partially digested fish are regurgitated and apportioned to the young. Later, one fish at a time is carried back to the nest, where it is consumed whole by a nestling. The male Belted Kingfisher feeds the young at least twice as much as does the female. Most feeding occurs in the morning and early evening, and the young may be unattended for up to 2.5 hours in the afternoon. In one study, it was found that each nestling, fed fingerling coho salmon (*Oncorhynchus kisutch*), required an average of eight fish daily, the figure rising to eleven at the period of peak growth.

For the first two weeks of life, young Common Kingfishers manage to obtain equal shares of food by means of a strict queuing system. The young sit in the nest-chamber, in a circle, with their bills pointing outwards. When the adult brings a fish into the nest, only the chick facing the tunnel gapes, calls and receives the fish, the other chicks remaining passive. The chick



Laughing Kookaburras often breed in groups, consisting of a pair and several of its earlier male offspring. All members of the group participate in the feeding and brooding of the chicks in the nest, characteristically located in a tree hole or an arboreal termitarium, and studies have shown that helpers provide up to 61% of food brought to the nest. The male shown here, identified as such by the amount of blue on its rump, could, therefore, be either the breeding adult or one of the pair's helpers.

[*Dacelo novaeguineae*  
*novaeguineae*,  
Goomborian, south-east  
Queensland, Australia.  
Photo: Cyril Webster]





This photograph of a Common Kingfisher demonstrates how the adult, when bringing food back for its young in the nest, carries the fish appropriately positioned in its bill, with the head facing outwards. This will enable the meal to be passed immediately to one of the hungry chicks, which can then swallow its food head first in the normal manner. As is the rule among the Alcedinidae, both parents feed the young. This familiar species, perhaps the best-known of all members of the family, provides its brood with small fish, only 1-2 cm long, for the first few days; as the chicks grow, it brings in slightly larger fish, generally up to about 8 cm in length but occasionally bigger. Each of the young kingfishers receives a feed every 45-50 minutes in the initial stages of life, this rate gradually increasing as the young grow until, at the age of 18 days, not long before leaving the nest, a chick can expect to be fed once every quarter of an hour or so. Incidentally, it is common for many alcedinids, including the Common Kingfisher, to bathe after feeding, one reason probably being the unhygienic conditions inside the nest-chamber.

[*Alcedo atthis ispida*,  
Toledo, Spain.  
Photo: Francisco Márquez]





It is interesting to look at the way in which a kingfisher manoeuvres its body as it approaches its nest in rapid flight. This is perfectly illustrated here by a Common Kingfisher alighting at its nest in a vertical mud bank. When the bird comes to within 30 cm or so of the nest-hole, it drops its legs and spreads its wings, these appendages acting as an effective brake to slow it down. Clamping its feet on to the lower rim of the hole, it assumes an involuntary arched posture with the body, whereby the head and neck project well forward with the momentum of the bird's movement. Once the kingfisher has gained a firm toehold, its wings are used for balance as it steadies itself before entering. Of course, much of this sequence is not so easy to appreciate when it happens at normal speed. If the bird, having landed, needs then to reach its family in the nest-chamber, it will immediately shuffle quickly along the tunnel in a hunched posture. In the latter stages of the nestling cycle, however, it need proceed no farther than the entrance, because older young make their way there and wait for the arrival of a parent with food.

[*Alcedo atthis ispida*,  
Toledo, Spain.

Photos: Francisco Márquez]

that has been fed then retires to the back of the chamber, and the circle rotates, so that another chick is now facing the entrance and will receive the next fish to be delivered. Any chick trying to obtain food out of turn is pecked vigorously by the others, and is sometimes even tossed backwards. After two weeks, this system changes, and the young face forwards in overlapping rows, begging in the manner of adult females, with shivering wings. Towards fledging, as rivalry increases, this sequential feeding breaks down and young move down into the tunnel to be fed. The young kingfishers usually leave the nest all on the same day, at intervals of ten to 20 minutes, and fly to a nearby perch, where they wait to be fed. Later, they follow the parents to their fishing sites. Although fed by the parents for two to four days after fledging, they start to dive on the first day. Their fishing success rapidly improves, and they are soon independent.

In the Blue-winged Kookaburra, it is the parental male, together with any male helpers that may be present, that is mostly responsible for the feeding of the nestlings in the initial stages. Later, as there is less need for brooding, the female increases her supply of food to the young. White-throated Kingfishers bring in fish and frogs head first, entering the nest-chamber to feed small young, but later the older nestlings move along the tunnel to meet the adults, and when close to fledging they come right to the entrance.

On hatching, young Belted Kingfishers are bright pink with a blackish bill. They lack natal down, and their eyes are closed. Feathers on the humeral tract first emerge by the sixth day, but the major wing and tail feathers remain sheathed until the last ten days of the nestling period. Growth rates are highest during the first ten days, and by 16 days the chicks are at adult body weight, but they lose some weight by the time of fledging. This is because, during the last three or four days, the adults bring less food to the nest. Fledglings leave the nest usually about 28 days after hatching. An adult, with a fish in its bill, will call to the young from a nearby perch, encouraging them to leave the nest-tunnel. They respond with begging calls from the burrow entrance. Fledglings stay with their parents for about three weeks, and are fed by them. Initially, the young take crayfish and aquatic insects, and at least a week elapses before they take the first fish. This contrasts with the situation of the Common Kingfisher, fledglings of which become independent within a few days of leaving the nest, by which time the adults are frequently occupied with raising the next brood.

With the exception of the Common and Belted Kingfishers and a few other well-studied species, the growth rates of nestling kingfishers are not known in detail. Hand-reared Pied Kingfishers showed a mean daily growth of 4.3 g over seven days in the period of linear growth.

Although the available information is scant, most of the Alcedinidae are single-brooded. The Belted Kingfisher, for instance, normally has just one brood, but it may lay a second clutch if the first is destroyed. Some species occasionally raise a second brood, the Pied Kingfisher being one such example. Second broods are regularly reared, however, by the Sacred, the Red-backed, the Azure and the Blue-eared Kingfishers (*Alcedo meninting*), as well as by the Oriental Dwarf-kingfisher. The Common Kingfisher normally has one or two broods, but occasionally three or four. Another *Alcedo* species, the Malachite Kingfisher of the Afrotropics, has three or four broods and is capable of achieving remarkable productivity: one pair raised 14 young over a period of just 4.5 months.

Sexual maturity is reached in the first year of life in the cases of the Pied, Common and Belted Kingfishers. This is presumably the age at which the majority of alcedinids first breed, although reliable data are lacking for most species. Laughing and Blue-winged Kookaburras are sexually mature at one year of age, but most will not start breeding until several years later.

Some young Belted Kingfishers return to breed in the general area in which they were reared, but most are not seen again. While some adults revisit and use nesting sites where they have previously bred successfully, many do not, suggesting either high mortality or a weak attachment to the nest-site. In the Pied Kingfisher, females seem to disperse more than do males. In several



Adult kingfishers feed their young on a diet that is little different from what they themselves eat.

This Brown-hooded Kingfisher, a species which lives mainly on invertebrates but also takes a fair number of vertebrate prey, including amphibians, reptiles, young birds and small rodents, is delivering a snake for its brood. Although this kingfisher usually excavates a tunnel in a bank or road cutting, it also makes use of a variety of other sites, such as old woodpecker holes and, occasionally, holes in colonies of sand martins (Riparia) or bee-eaters (Merops). Nests among rock cavities, as here, would seem, however, to be more unusual.

[*Halcyon albiventris albiventris*, near Mtunwini, South Africa.

Photo: Nico Myburgh]

studies of this species, no yearling females were recorded returning to their natal colonies, and fewer adult females returned to the colony than did adult males. Female Common Kingfishers are more likely to disperse away from their breeding sites, while males tend to remain there.

Breeding success varies considerably among different species of kingfisher, and even among different populations of the same species. Hatching success of Pied Kingfishers in East Africa was found to be between 90% and 94%; as mentioned above, however, the percentage of hatched chicks that fledged varied from 39% at Lake Victoria for pairs with no helpers, to 80% at Lake Naivasha for pairs with no helpers, and to 100% at Lake Victoria for pairs with two helpers. Considerable individual variation was found also among breeding pairs of Buff-breasted Paradise-kingfishers in Australasia: one female raised four young in each year for two successive years, while only three out of nine eggs hatched in other nests. In Minnesota, USA, over four breeding seasons, the hatching success of the Belted Kingfisher was nearly 87% and the fledging success was 97%.

From various studies carried out over a number of years, the overall breeding success of the Common Kingfisher was 80% in Britain and 54% in Switzerland. In Britain, the species' average annual mortality in the first year of life was 77.8%, while its average annual adult mortality was slightly lower, at 76.2%.

Most kingfishers escape the attention of brood parasites. In Africa, however, the Greater (*Indicator indicator*) and Lesser Honeyguides (*Indicator minor*) parasitize species which nest in tree holes, such as the Striped, Grey-headed and Brown-hooded Kingfishers, and also the bank-nesting African Pygmy-kingfisher.

Although kingfisher nests are usually fairly inaccessible, many predators do try to attack them. Red foxes (*Vulpes vulpes*) and introduced American minks (*Mustela vison*) are the main nest predators of the Common Kingfisher in Sweden, and both dingoes (*Canis lupus*) and foxes will dig out the nest-chambers of Red-backed Kingfishers in Australia, eating the contents and, sometimes, the adult bird as well. Skunks (*Mephitis mephitis*) dig into the nest-chambers of Belted Kingfishers, while minks and raccoons (*Procyon lotor*) gain access via the nest-tunnel. In

Gabon, even chimpanzees (*Pan troglodytes*) have been known to raid Blue-breasted Kingfisher nests built in arboreal termitaria. Snakes, including, among others, *Elaphe* species, not infrequently find rather easy access to kingfisher nests, where they eat the eggs and young. An olive python (*Liasis olivaceus*) which entered the nest of a pair of Blue-winged Kookaburras constricted and ate two of the three chicks, and at another nest the same species of snake swallowed the incubating female, which, to judge from the external wounds on the python, had apparently put up a struggle. Monitor lizards (*Varanus*) frequently break into the nests of Buff-breasted Paradise-kingfishers. For the Pied Kingfisher, causes of mortality, other than the collapsing or flooding of nest-tunnels, include the activities of such nest predators as driver ants (*Dorylus nigricans*), the monitor lizard *Varanus niloticus*, cobras (*Naja*) and mongooses (*Herpestes* and *Atalax*).

Spirited defence of the nest is a characteristic of several species of alcedinid. Forest Kingfishers, for example, violently attack goannas or snakes that approach near the nest. The Yellow-billed Kingfisher, too, is very aggressive in defence of its nest. One attacked an egg-collector, hitting his hand and drawing blood; the collector left the eggs to the "plucky little beggars". Moreover, bird-photographers, while building the hide, have also been repeatedly hit on the head, and even under the brim of a hat, by this same species.

As a whole, kingfishers are quite long-lived birds. The records for longevity for those species for which information is available are 15 years and 5 months for the Common Kingfisher, 11 years and 6 months for the Laughing Kookaburra, 8 years for the Sacred Kingfisher, and nearly 8 years for a Giant Kingfisher. In captivity, a Laughing Kookaburra lived for over 15 years.

## Movements

Many species of kingfisher seem to be resident, and the dispersal of juveniles away from the breeding place is their only obvious movement. An example of this is provided by the Common Paradise-kingfisher of New Guinea. It is highly sedentary and, in some areas of primary forest, a pair can live throughout the year within



the boundaries of a territory of 0.3-0.5 ha. The Laughing Kookaburra is also sedentary throughout the year, but it may move short distances in order to exploit good sources of food. Non-breeding kookaburras may, prior to the breeding season, disperse 50-100 km in their search for a mate and a vacancy in an established territory.

Nevertheless, there are some other alcedinids that show definite patterns of movement. These can be complex, with considerable variation even within the same species. The Buff-breasted Paradise-kingfisher has two subspecies in New Guinea, both of which are probably sedentary. A third subspecies, however, is a regular migrant between its breeding grounds in the forest of northern Queensland, in Australia, and its non-breeding quarters in southern New Guinea. Some of these birds migrate over the relatively narrow Torres Strait that separates Australia from New Guinea, a distance of 150 km, but others may take a more direct route across the Coral Sea to reach south-east New Guinea, which involves the crossing of a much broader stretch of water. The kingfishers seem to migrate in flocks, and, on the northward migration, adults leave separately from the young of the year. The females, at least, return to the same breeding territory in Queensland for a number of years in succession.

Northern populations of the Common Kingfisher are chiefly migratory, being forced to leave their summer range as the water freezes in winter, while those in central Europe move only in severe winters. Populations in the south and west are, for the most part, resident. Of these, the birds most likely to move are immatures, followed by adult females. For the western and central populations, these movements take them mainly to southern Europe, North Africa, Arabia, Pakistan and north-west India, while the eastern populations breeding in Siberia and China migrate to southern Asia, the Philippines and Indonesia. After fledging, most young Common Kingfishers disperse from the natal territory, apparently without any preferred direction, and for distances varying from tens to hundreds of kilometres.

Over much of its range in North America, the Belted Kingfisher is a partial migrant. It moves to Central America and the West Indies in winter, although a few individuals overwinter in

the breeding range, particularly on the coasts, and in the south-east. During migration, these birds fly along lakeshores and up major river valleys. At the height of the spring passage, in mid-April, twelve to 15 birds per hour can pass along the shores of the Great Lakes.

These patterns of movement can become more complicated for species which have populations breeding both north and south of the equator. The Woodland Kingfisher is one such example. This species is sedentary in equatorial forests, and populations living in savanna are also sedentary within about 8° north and south of the equator. At higher latitudes, however, Woodland Kingfishers become progressively more migratory, being breeding visitors to the Sahel zone of West Africa during the northern summer, from July to October, and also visiting southern Africa to breed there during the austral summer, in September-April. In the austral winter, some of these southern breeders move as far north as Sudan. The African Pygmy-kingfisher exhibits a similar pattern of movement, with southern breeders also migrating north to Sudan in winter, this flight of over 2500 km being a remarkable one for a bird weighing less than 20 g.

The Grey-headed Kingfisher, another Afrotropical species, has even more complex movements, which vary considerably from area to area and among the different subspecies. Populations in the Cape Verde Islands, in equatorial Africa and in coastal East Africa seem to be resident, but populations to the north and south show more definite movements. The population in Arabia is present from April to mid-December, and probably spends the winter months in Somalia. Ethiopian breeders migrate south to East Africa, two individuals having been recorded as travelling, respectively, 960 km to Uganda and 1750 km to Kenya. The Grey-headed Kingfishers in the southern tropics breed in the austral summer and then move north in April-May to Kenya, Rwanda and Burundi, returning south again in August and September, but in Zambia and Malawi some remain over winter. One individual ringed in Malawi was recovered 1430 km away, in Zaire. In West Africa, this species' movements are even more complex. In that region, southern populations near the coast breed in the dry season, during January and February, and migrate north

A centipede would appear to be a somewhat unusual food item for a Forest Kingfisher to bring to its brood. At one nest of this Australasian species, which is sometimes a co-operative breeder having several helpers, a brood of two chicks accepted a daily ration of 12-20 fish, frogs and lizards. Surprisingly, however, the same nestlings rejected any insects that were offered to them.

[*Todiramphus macleayii*  
*incinctus*,  
Goomboorian, south-east  
Queensland, Australia.  
Photo: Cyril Webster]





The Malachite Kingfisher is a common bird throughout its sub-Saharan African range, where it nests mainly in streamside banks. Other frequently used sites include road cuttings, pits, and mounds of earth, and this species will often excavate a tunnel in the soft soil in the roots of a fallen tree. This is one of several alcedinids that are capable of raising more than one brood in a season. In fact, this small kingfisher regularly rears three or four broods and, as a consequence, is able to achieve high productivity; in Kenya, for example, one pair raised a total of nine young from three broods over a period of just four months. Since the combined incubation and fledging periods of this attractive kingfisher amount to about one month, this means that the adults must work ceaselessly in order to attain this level of success.

[*Alcedo cristata cristata*,  
Lake Baringo, Kenya.  
Photo: Günter Ziesler]





Another common Afrotropical species, the Woodland Kingfisher usually nests in a tree cavity, often an old nest of a barbet (Capitonidae) or a woodpecker (Picidae), at an average height above ground of 5 m. This individual had selected a site about 6-7 m up. In South Africa, where this photograph was taken, the Woodland Kingfisher is largely migratory; after breeding in September-April, many of the population then migrate north, some reaching as far as Sudan. A similar migratory pattern occurs in the sahel zone of West Africa, where the breeding season is July-October, but the species is resident in the equatorial belt.

[*Halcyon senegalensis*  
*cyanoleuca*,  
near Naboomspruit,  
South Africa.

Photo: Cyril Laubscher]

for the wet season, while northern populations in the Sahel zone breed in the July-August wet season and migrate south for the dry season. It is not known whether the kingfishers involved represent discrete populations or whether the same individuals breed twice a year. Populations of Grey-headed Kingfishers at middle latitudes have a three-stage migration that is more complicated still: they breed from March to June, and then move to the far north, moulting there in the July-August wet season, following which they migrate to the far south for the dry season, before finally returning north to their breeding grounds. In Nigeria, the peak of juvenile migration is one to two weeks later than that of adults.

The Oriental Dwarf-kingfisher of South-east Asia is another small species which has complex movements. Rufous-backed and black-backed forms hybridize readily in Borneo, in Sumatra and in southern Peninsular Malaysia, but in the last region there is little hybridization between the two forms north of Kuala Lumpur. There, the red-backed form is sedentary, whereas the black-backed form migrates south in August-September and returns north in March. During the migration period, hundreds of these little kingfishers can arrive at night at hill stations, and even on islands 60 km out to sea.

Some species exhibit more irregular movements. The Red-backed Kingfisher is migratory in southern parts of Australia, arriving in spring to breed and then leaving in autumn, while in northern Australia it is present throughout the year, with an influx of southern birds recorded there in winter. In central parts of Australia, however, its presence is more erratic, with individuals arriving in some areas after good rain and then moving north or east in drought years.

Migrating kingfishers often fly at night, and large numbers are sometimes killed when they fly into windows, towers and buildings. The Belted Kingfisher migrates primarily during the day, but there are reports of individuals being killed overnight at

a lighthouse on the Florida Keys, in the south-east USA, which indicates that nocturnal movements also occur.

### Relationship with Man

Many kingfishers are rather shy birds, which are seldom kept in captivity, and most humans would probably be quite unaware of their presence or activity. Despite this, the bright colours and interesting habits of a few of the species have brought them greater attention.

The English word "kingfisher" comes from two traits displayed by the Common Kingfisher, namely its "royal" blue colours and its fishing habits. Similar descriptives are used in many languages. The French *martin-pêcheur* means a fishing bird, and the Zimbabwean chiShona expression *kanyururahove* for the Malachite Kingfisher can be translated as a "small diver for fish". The Common Kingfisher, woodpeckers (Picidae), wrens (*Troglodytes*), crows (*Corvus*) and robins (*Erithacus*) were all considered sacred to St Martin, the holy gravedigger and bringer of winter, and both woodpeckers and the kingfisher have a wintery and phallic connotation in European mythology.

Kingfishers figure prominently in Greek mythology. Alcyone was the daughter of Aeolus, the keeper of the winds, and she married Ceyx, the king of Trachis, who was later drowned at sea. The gods metamorphosed both Ceyx and his grieving wife into a mythical bird, named halcyon, which nested on the sea. The gods calmed the seas while the birds incubated the eggs and raised their young each year, and such calm days have become known as "halcyon days". Halcyon has generally been associated with the Common Kingfisher, although some authors maintain that it could refer to a shearwater or petrel (Procellariidae). A similar association with the sea is responsible for the Sacred Kingfisher's name. Together with other Pacific kingfishers, it





For most of the well-studied alcedinids, it has been found that both sexes feed the nestlings. Such is the case with the Sacred Kingfisher, the young of which receive food from both parents in roughly equal amounts; here, a well-grown nestling is being fed a grasshopper by the male parent. This species, incidentally, is particularly aggressive towards any intruders near its nest, and will launch violent assaults on other birds, including other alcedinids, as well as attacking large reptiles and mammals; cats and dogs have reportedly been blinded, or even killed, by this kingfisher. A noteworthy aspect of the Sacred Kingfisher's life is the long-distance migrations of the south Australian population, most of which, after breeding, move north to New Guinea and the Indonesian islands, juveniles sometimes preceding adults, and covering distances of up to 4000 km. Ringing studies have shown that individuals return to the same breeding sites in successive years.

[*Todiramphus sanctus sanctus*, Warumbungle National Park, New South Wales, Australia. Photo: W. R. Taylor/Ardea]

was venerated by the Polynesians, who believed it to have power over the waves and the ocean.

Pied Kingfishers are often conspicuous in early Egyptian illustrations of marsh scenes from the fifth, sixth and eleventh dynasties. The Common Kingfisher is less frequently depicted in these scenes. In modern times, the children of fishermen often keep young Pied Kingfishers as pets in eastern Nigeria. The birds very rapidly become tame and move around with the children, eventually returning to the wild or ending up, unfortunately, in a cooking pot.

In New Guinea, the striking yellow head of the Yellow-billed Kingfisher is greatly prized by people of the Middle Sepik River. Having captured and killed several birds, they clean the heads and mount them on sticks, and then wear them in their hair like hat-pins. Again in New Guinea, the plumes of the *Tanysepta* paradise-kingfishers are used as decorations in the ceremonial head-dresses of highlanders, and the name of these birds, *joly*, is sung in beauty-magic chants. The calls of two other halcyonines, the Shovel-billed Kingfisher, known colloquially as *plag*, and the Mountain Kingfisher, or *plotom*, are both considered to be signs of good weather.

Among the Dusun people of Borneo, a "forest" kingfisher known as the *mantis raa*, which is probably the Oriental Dwarf-

kingfisher, is regarded as a formidable bird of omen. If a warrior sees one on his way to battle, he must return home immediately or face serious illness. The Ibans of Borneo consider *embuas*, the Banded Kingfisher, to be an omen bird, but generally a favourable one, and particularly so if it calls to the right-hand side of the person who hears it.

The bright plumage colours of many kingfishers also made them a favourite among Victorian bird-collectors. Various species were often to be found with other colourful birds, such as parrots (Psittacidae), hummingbirds (Trochilidae), bee-eaters or pittas (Pittidae), in an ornamental display under a protective bell-jar. In present-day Europe, with somewhat more enlightened attitudes towards bird conservation, such practices are generally frowned upon, although some old collections may still contain such specimens.

A South American legend from the Arawak tribe of Guyana tells of a Ringed Kingfisher and a Grey-winged Trumpeter (*Psophia crepitans*) having a fight and falling into the ashes of a fire, resulting in the grey coloration of those two species. Kingfishers also appear in several North American tales. One, from the Sioux Indians, relates the story of a kingfisher diving to obtain fish for a visitor, Ictinike, son of the sun-god; later, when the kingfisher visits Ictinike, the god also tries to catch fish by div-



Adult White-throated Kingfishers, as those of other alcedinids, carry fish and frogs head first when bringing these prey to the nest. When the young chicks are still small, the feeding parent enters the nest-chamber; later, the older nestlings will meet the adult in the tunnel, and they wait at the entrance when close to fledging. Interestingly, the parent kingfishers smash the shells of crabs before delivering these to their young, thus illustrating how important it is that such prey items be adequately treated before being consumed. This photograph also shows how easily indigestible food remains can build up inside the nest.

[*Halcyon smyrnensis fusca*,  
Sri Lanka.  
T. S. Zylva/FLPA]



ing and has to be rescued from drowning by the bird. Other stories, from the Arikara tribe on the Missouri River, describe a kingfisher flying at banks and making them collapse, enabling Mother Corn, the mother of the tribe, to lead her people on various journeys.

Probably the world's most famous kingfisher of all is the kookaburra. In Australia, the Laughing Kookaburra is one of the best-known of all native birds. The name "kookaburra" is an Aboriginal word, first recorded by Governor Phillip in 1789, and it was used in over 40 variants along the east coast of Australia. One Aboriginal myth is that, when the world began, there was no light and dark, but just a grey twilight. After the gods had made day and night, they appointed the kookaburra to be sentinel of the morning, using its loud, raucous call to wake people and animals at the start of each day. For similar reasons, the early European settlers in Australia called the kookaburra the "settlers' clock". They also used the name laughing jackass, referring to the bird's call and its "unkempt" appearance.

The kookaburra is a bold, confiding bird, common in parks and large suburban gardens, and these features, together with its propensity for catching and killing snakes, perhaps including venomous ones, soon made it one of Australia's best-loved symbols. Many people thought that it reflected aspects of the

Australian character, and it reached its greatest popularity in the 1920's and 1930's. The kookaburra featured in numerous commercially registered trademarks for items as diverse as tea and cricket balls. It was the subject of songs, plays and children's books, and its image was found on stamps and coins, as well as on the crests of the Royal Australian Air Force bomber squadrons and Navy ships. During the First World War, in 1914-1918, postcards featuring a "Diggaburra" in military uniform, sent to the Australian troops, became a good-luck symbol. For many years, Australian Movietown News, shown at cinemas, was heralded by the call of the Laughing Kookaburra, and the bird's highly distinctive laugh is still often used in films to provide the atmosphere for "jungle scenes". The fact that this kingfisher is not a jungle denizen and is not found outside Australia does not seem to matter to the film-makers. Its popularity has waned somewhat in recent years as these images have been considered old-fashioned, but it remains a popular icon, still used by a national hockey team.

Kingfishers have few negative impacts on humans, but they do occasionally take fish that are considered "the property" of certain people. In the case of ornamental garden ponds, these losses either are tolerated or are discouraged by the placing of netting over the ponds. At commercial fish farms, however, king-



fishers are often shot, legally or otherwise, and considerable numbers can be killed in this way.

### Status and Conservation

Kingfishers are faced with many forms of environmental pressure. A good number of their species live in primary forest, a habitat that has been subjected to unprecedented clearing in the ten to twenty-five years leading up to the end of the twentieth century. Other species live in small populations on small isolated islands, where relatively minor disturbances can threaten their survival. Habitat clearance and pollution can represent a threat even to widespread species.

For many of the Alcedinidae, there is a paucity of accurate and recent information on their biology and conservation status. This applies particularly to many of the forest-dwelling species. Eleven members of the family are currently considered threatened by BirdLife International, with one subspecies of an additional species also placed in that category. Only one alcedinid, the Marquesas Kingfisher, is classified as Endangered. It occurs only on two small islands in the Marquesas, where its already much-reduced population may be declining further owing to deterioration of the upland forest which it inhabits, along with predation by introduced animals. On one of those two islands, Hiva Oa, the situation of the Marquesas Kingfisher is deemed to be critical. A further ten species are classified as Vulnerable. These are the Moustached and Blue-capped Kingfishers in the genus *Actenoides* and the Philippine Dwarf-kingfisher (*Ceyx melanurus*), along with four *Todiramphus* and three *Alcedo* species. The *Todiramphus* species are the Rufous-lored, Chestnut-bellied, Sombre and Tuamotu Kingfishers, and the Vulnerable *Alcedo* species are the Silvery, Blue-banded and Bismarck Kingfishers. In addition, the race *ruficollaris* of the Chattering Kingfisher, confined to the island of Mangaia in the Cook Islands and regarded by many as a distinct species, is also considered to be Vulnerable.

Some general trends are evident among these species. Most are very restricted in distribution, limited either by habitat or by



The normal clutch of the Blue-winged Kookaburra is two or three eggs, these hatching at one-day intervals. The largest chick may subsequently attack, and even kill, its younger siblings, using the hook at the tip of its bill. In the nest shown here, the situation in the early stages may seem unpromising; two of the eggs have yet to hatch, while the existing chick looks very fragile. Nevertheless, a full brood was reared, as shown by the three almost fully grown chicks in the lower photograph, taken later at the same nest. Two-thirds of breeding pairs of this species have helpers, or auxiliaries, the majority of which are males. These assist with most duties, including preparation of the nest, feeding of the female before laying, incubation of the eggs and feeding of the chicks. The parental male, and male helpers when present, provide most of the food for the nestlings in the initial stages; later, when there is less need for the chicks to be brooded, the female increases her share of this responsibility. Presumably, it is the amount of food that is available that determines whether or not siblicide occurs.



[*Dacelo leachii leachii*, Kakadu National Park, Northern Territory, Australia  
Photos: David Curl/  
BBC Natural History Unit]





From the very first days of their life, young Common Kingfishers have a huge appetite. With six or more chicks in the nest, it is important that each one receives sufficient food to enable it to grow, and this is achieved in a most interesting way. For the first two weeks, the chicks sit in the nest-chamber in a circle, each with the bill pointing outwards. On the arrival of a parent with a fish, only the chick immediately facing the tunnel gapes and gives the begging call, so it is that one which receives the food, following which it moves to the back of the nest-chamber. The circle then rotates, so that the next meal will go to the next chick in line, which repeats the same procedure. It seems that any chick which tries to "jump the queue" is viciously pecked by the others. After two weeks, however, when the young are bigger, they all face to the front in overlapping rows, and actively beg for food from the arriving adult. As they near the fledging stage, rivalry sets in and this orderly system breaks down; the young kingfishers then move down the tunnel towards the entrance, each trying to be the first to be fed as the adult brings in food. Finally, the whole brood leaves the nest on one day, with only short intervals between each.

A point of interest shown well here is the remarkable size of fish which young kingfishers are capable of swallowing; all the same, some items may on occasion be just a little too big.

[*Alcedo atthis ispida*,  
France.]

Photos: Bruno Cavignaux/  
BIOS]





geography, and the populations of all appear to be declining. Seven of the taxa are found in recently identified "biodiversity hotspots", where high concentrations of endemic species face exceptional loss of habitat. There are four Vulnerable species in the Philippines, the Blue-capped, Rufous-lored and Silvery Kingfishers and the Philippine Dwarf-kingfisher. Two more, the Marquesas and Tuamotu Kingfishers, are confined to Polynesia, as also is *ruficollaris*, while Wallacea harbours the Near-threatened Lazuli Kingfisher. Two other threatened species are found in adjacent areas, the Moustached in the Solomon Islands and the Chestnut-bellied Kingfisher in Vanuatu.

All but one of these kingfishers inhabits forest, and this habitat has suffered huge losses. In the Philippines, a mere 3% of the original primary vegetation remains, while in Wallacea only 15% survives and in Polynesia 21.8%. The exception is the single surviving race *gertrudae* of the Tuamotu Kingfisher, which is found in gardens and coconut groves, but that taxon is restricted to Niau Island, in the Tuamotu Archipelago. Many other kingfisher species, not yet listed as threatened, occur in the western part of Indonesia and Malaysia, the Sundaland region, where no more than 7.8% of the original primary vegetation is still to be found intact. With this massive habitat loss, it seems inevitable that more species will become threatened in the future, unless major conservation efforts are directed at saving the remaining natural habitat in these regions.

Twelve species are considered Near-threatened. The majority of these also have a small and restricted distribution. For example, the Lazuli Kingfisher, already mentioned, is found only on the Indonesian island of Seram. Blyth's Kingfisher differs from all the others, as well as from the threatened species, in that it has a very wide distribution, ranging from Bhutan and north-east India to Myanmar, south China, and central and northern Laos and Vietnam. It is found along streams in evergreen forest, mainly below 1000 m, and everywhere seems to occur at very low densities. Forest clearance, human disturbance and pollution are all possible threats to this kingfisher. Furthermore, in China, the construction of a hydroelectric scheme within the Che Ba Ling National Nature Reserve, in northern Guangdong, has resulted in the diversion of one stretch of the river for some 3 km, along with the destruction of forest on one side of the river, and increased human access through a new road. It is calculated

that up to 40% of the river used by Blyth's Kingfishers will now become unsuitable for the species.

Kingfishers living on isolated islands face particular problems, because their populations, once reduced, are unlikely to be replenished from other sources. They are subject to a number of threats, the most important of which are probably forest clearance by humans or damage by natural cyclones. Two kingfishers have become extinct in recent times, although it is debatable whether they were subspecies or full species. One, the Mangareva, Gambier or Tuamotu Kingfisher, has been variously treated as the nominate race of the Tuamotu Kingfisher, or as a subspecies of the Chattering Kingfisher, though it might alternatively be listed as a full monotypic species (see Systematics). It was found on Mangareva Island, in the Gambier group of the Tuamotu Archipelago, in Polynesia, and probably became extinct before 1922. The other extinct form, *miyakoensis*, was probably a subspecies of the Micronesian Kingfisher, though it is thought by some to have been a full species. It is known only from a single specimen, taken on the island of Miyako-jima, in the Ryukyu group, the southern chain of Japan that extends almost to Taiwan.

Most alcedinids are not sufficiently well known to be used as the focus for conservation efforts, and so their protection must rely on general programmes for forest conservation and clean water. Many species are at the top of the aquatic food chain, a fact which makes it likely that they will accumulate toxins in their body tissues. This has led to the suggestion that species such as the Common Kingfisher could be used as highly visible bioindicators, to monitor the health of waterways.

Many chemical toxins, the result of industrial effluent or of agricultural herbicide or pesticide use, find their way into rivers and lakes. It is not, therefore, surprising that kingfishers often have significant levels of these chemicals in their body tissues. In Britain, Common Kingfishers monitored over a 27-year period, from 1963 to 1989, had significant levels of the organochlorine pesticides HEOD and DDE, polychlorinated biphenyls (PCB's) and mercury in the liver, but the levels of all of these declined over the period as the use and disposal of such biocides have been more rigorously controlled. The kingfisher's numbers also showed declines early in that period, but this may have been caused more by several severe winters than by pesticide toxicity.

In the USA, Belted Kingfishers collected from the Sheboygan River, in Wisconsin, which had been polluted by industrial run-off, had detectable levels of several toxins. In post-mortem examinations, their tissues were found to contain dieldrin at 0.6-1.5 parts per million (ppm) wet weight, DDE at 2.4-8.8 ppm, and particularly high levels of PCB's, measured at 65-218 ppm. The PCB's were at concentrations that would cause significant impairment of reproduction in domestic hens, but their impact on the kingfishers is unknown.

A further example of environmental pollution comes from Africa. Spraying of the organochlorine insecticide endosulfan to control tsetse flies (*Glossina*) in the Okavango Delta of Botswana led to the death of some fish. These attracted Pied Kingfishers, which fed on the debilitated fish until this resource was depleted, causing some of the birds to leave the area. Fortunately, however, the local Pied Kingfisher population survived the spraying, and the numbers at a communal roost remained steady. Endosulfan residues were detected in kingfisher body tissues, but at concentrations no higher than those present in the fish, indicating no accumulation there.

As already mentioned (see Relationship with Man), some kingfishers are killed for their bright and colourful plumage, and kingfisher plumes are used in traditional costumes in the highlands of New Guinea. They may also be procured for the tourist trade, sometimes in surprisingly high numbers. For example, 40 stuffed Ruddy Kingfishers were found in a Taiwanese taxidermist's shop. On this scale, this kind of activity could have far-reaching effects on some kingfisher populations.

Managers of fish hatcheries often consider that large, conspicuous birds and those with reputations as "fish thieves", such as herons (Ardeidae) and kingfishers, are responsible for most of their fish losses. Thus, the Belted Kingfisher was among the

Although having a small range, restricted to some ten islands in the Northern Maluku EBA in Indonesia, the Blue-and-white Kingfisher appears to be reasonably common. Its natural habitat is lowland secondary woodland and mangrove edges, but it seems to have adapted well to human disturbance and cultivation. It can now be found, for example, in wooded gardens, orchards and lightly wooded cultivated areas, including coconut groves. Its biology and ecology, however, require study.

[*Todiramphus diops*, Tanah Batu, Putih, Halmahera. Photo: Bernard Van Eiegem]





Three near-threatened kingfishers are restricted-range species of Sulawesi, being confined to that island and, in two cases, also Sangihe and the Talaud Islands to the north of there. All inhabit primary lowland forest below 1000 m, a habitat which has, in recent decades, been destroyed over extensive areas within the altitude range within which these three alcedinids live.

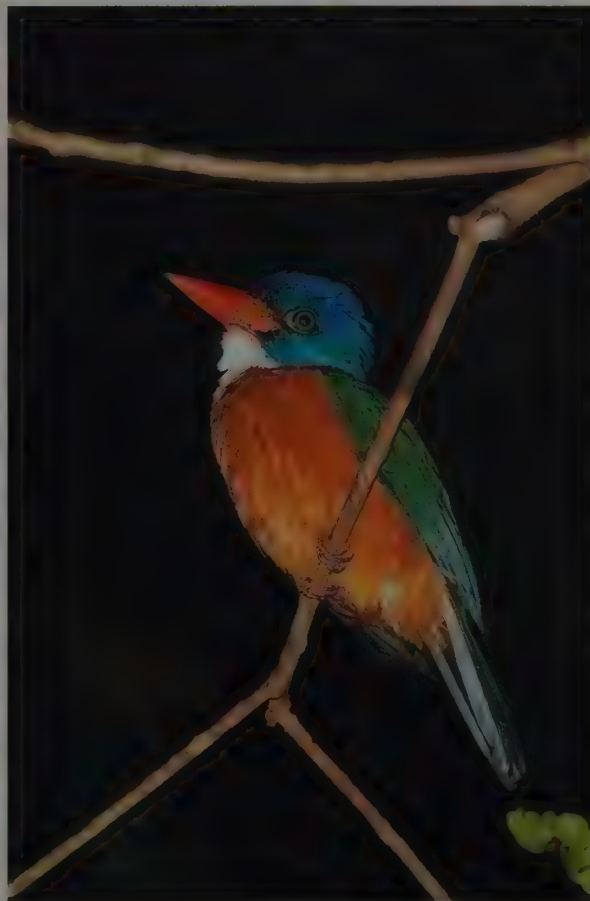
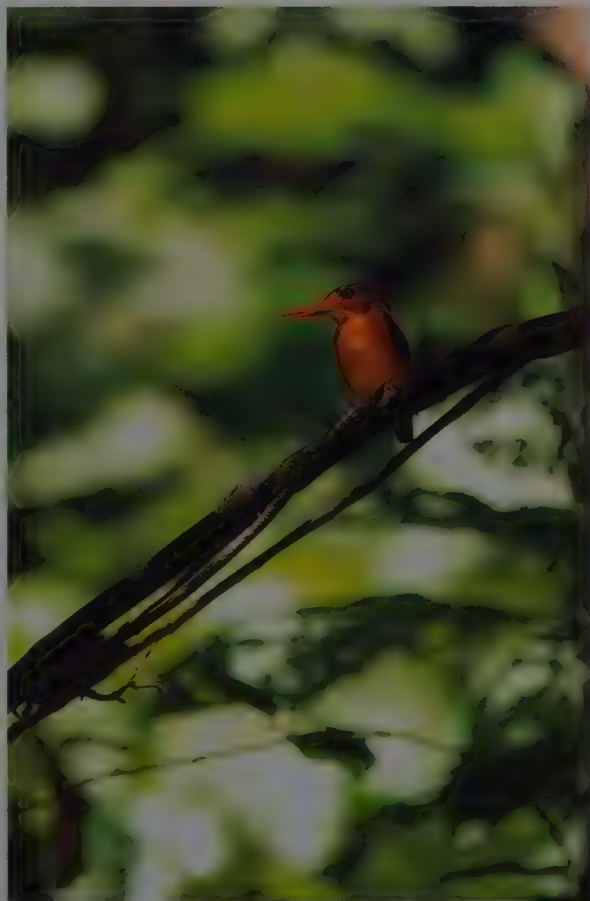
Each one is thought to have suffered a drastic decline in its population as a result, although localized pockets may contain somewhat higher numbers. Geographical races of both the Lilac-cheeked Kingfisher and the tiny Sulawesi Dwarf-kingfisher occur on Sangihe and the Talaud Islands, but the latter species may well be extinct on Sangihe.

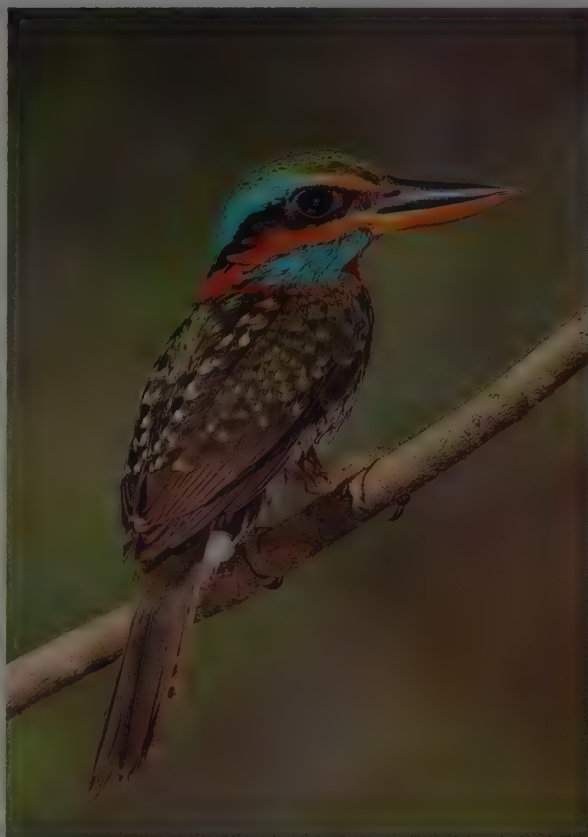
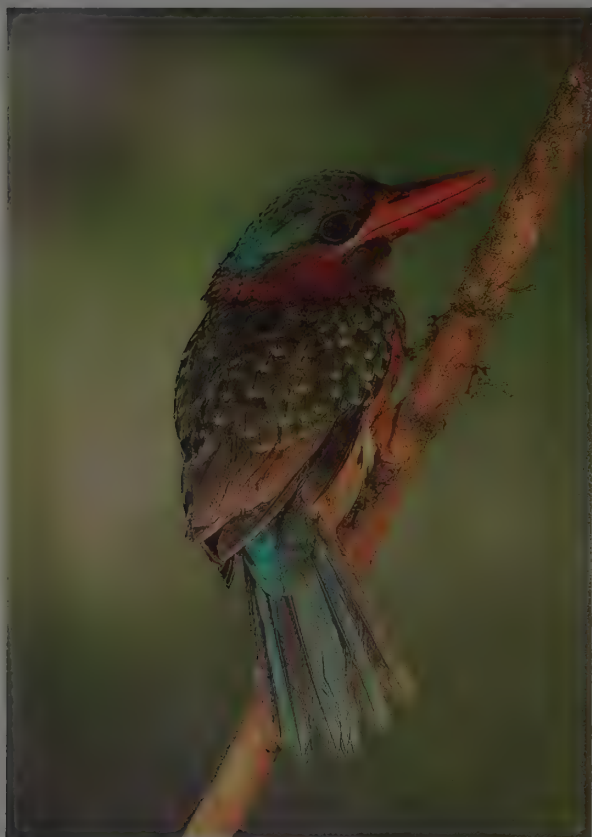
In common with the Lilac-cheeked Kingfisher, the Green-backed Kingfisher, the two races of which are restricted to the main island of Sulawesi, sometimes extends into tall secondary forest in the lowlands. This third species is possibly somewhat commoner than observations suggest, since it can often be highly inconspicuous. Nevertheless, continued loss of habitat could render all three of these kingfishers vulnerable.

[Above:  
*Cittura cyanotis cyanotis*,  
Tangkoko DuaSudara  
Nature Reserve,  
north-east Sulawesi.  
Photo: Bernard  
Van Elegem.]

Below left:  
*Ceyx fallax fallax*,  
Tangkoko DuaSudara  
Nature Reserve,  
north-east Sulawesi.  
Photo: Tui De Roy.

Below right:  
*Actenoides monachus monachus*,  
Tangkoko DuaSudara  
Nature Reserve,  
north-east Sulawesi.  
Photo: Bernard  
Van Elegem]





Forest clearance has seriously affected many species. The secretive Blue-capped Kingfisher, found only on Mindanao, in the Philippines, now has only a small, fragmented population and is considered Vulnerable. Its future survival may depend on key sites being afforded protected status. The similar Spotted Kingfisher of the north and central Philippines, once thought conspecific with the Mindanao species, can tolerate some habitat disturbance, but it, too, could easily become threatened.

[Left:  
*Actenoides hombroni*,  
Davao city, Baracatan,  
Mindanao, Philippines.

Right:  
*Actenoides lindsayi*  
*lindsayi*,  
Mount Maquiling,  
south Luzon, Philippines.

Photos: Doug Wechsler/  
VIREO]

top three birds that were considered predators of fish at eastern US hatcheries. Before protective legislation was introduced, this led to widespread shooting of kingfishers at fish farms. Over 400 Belted Kingfishers were shot or trapped during a single spring migration at a hatchery near Lake Michigan, and a total of 5568 kingfishers was reported killed at 174 fish hatcheries in Michigan in 1937. Many owners of fish farms continue to shoot and trap kingfishers, either under licence or illegally, but the impact on Belted Kingfisher populations does not seem to have been great. Moreover, despite this persecution, recent de-

tailed studies at trout (*Salmo*) hatcheries in Pennsylvania have shown that Belted Kingfishers accounted for a much smaller proportion of losses there than those attributed to many other avian predators.

In New Zealand, Sacred Kingfishers have been considered a nuisance for their attacks on bees, poultry, cagebirds, and goldfish (*Cyprinus*) or trout fry, as well as for damaging the fruit in cherry and peach orchards. The extent of such behaviour is uncertain, but it seems likely not to be great. Nevertheless, the kingfishers have sometimes been shot as a result of their alleged depredations.

Some kingfishers have benefited from man's activities. As an example, the clearing of forest has been beneficial for the White-throated Kingfisher in Malaysia. This species has utilized low-lying oil palm plantations, and reaches its highest densities in these habitats; as a result, it has increased in numbers and range over the last few decades. Laughing Kookaburras and Sacred Kingfishers are often found in open suburban gardens and parks in eastern Australia, where they find such man-altered habitats well suited to their ecological requirements. In the mallee shrubland of central Australia, there are few suitable nest-sites for Red-backed Kingfishers; when trees were knocked over for road construction, however, the soil remaining around their roots provided such sites and allowed the local population of kingfishers to increase. Similarly, in North America, the pits created by the extraction of sand and gravel have provided additional nesting sites for the Belted Kingfisher, which has resulted in local expansions of range and increases in population size of that species. On the other hand, one important consequence of clearing forest is the removal of many old trees with their associated holes, which provide nesting sites for many species of kingfisher. This problem is compounded by introduced species of bird, such as the Common Starling, the Common Myna (*Acridotheres tristis*) and sparrows (*Passer*), which evict kingfishers from the few remaining nesting hollows. This has been a particular problem for the endangered Marquesas Kingfisher and the vulnerable Mangaia subspecies *ruficollaris* of the Chattering Kingfisher.

Human artefacts can also lead indirectly to greater mortality among kingfishers. Many individuals of the migratory species

Another Vulnerable and rapidly declining kingfisher of the Philippines is the Silvery Kingfisher, which lives along open forested lowland streams. Widespread deforestation, coupled with pollution of watercourses, has reduced its numbers considerably, and its conservation requires the protection of important sites, some of which are currently becoming seriously degraded. Details of this shy species' ecology also need to be determined.

[*Alcedo argentata*  
*argentata*,  
Malagos, Mindanao,  
Philippines.  
Photo: Doug Wechsler/  
VIREO]





While the Micronesian Kingfisher is fairly common on the Palau Islands, its three other subspecies have not fared so well. The Ryukyu race, known from a single specimen, is extinct. The Carolines population survives, but in reduced numbers. In the Marianas, the nominate race has suffered from habitat loss and from predation by introduced tree-snakes; an estimated 150 pairs in the mid-1970's plummeted to just 30 individuals a decade later, and to extinction by the end of the century. Conservation efforts are centred on breeding the nominate race in captivity, with the hope of returning a viable population to the wild.

[*Todiramphus cinnamominus cinnamominus*,  
Guam.

Photo: Roland Seitre/  
BIOS]



are killed by hitting windows, buildings, lighthouses and street lights during their passage movements. Motor vehicles, too, can also inflict a significant mortality on some species. This is demonstrated by the fact that six Blue-winged Kookaburras, representing as much as 13% of the local population, were killed on a 3-km stretch of road in northern Australia.

A number of kingfisher species have been bred successfully in captivity. Most of these have involved common species, but a

successful breeding programme that has been carried out for the Micronesian Kingfisher may enable that species to be reintroduced to Guam and other Pacific islands. Its populations on several islands have declined as a result of forest clearance and the depredations of the introduced brown tree-snake (*Boiga irregularis*). Before any reintroduction can take place, there is a need for adequate measures to be drawn up to control the snake populations.

The Laughing Kookaburra is the only species of kingfisher to have been introduced to areas outside its normal range. Hundreds were brought from Victoria to Western Australia from about 1897, and the kookaburra was well established in the south-west by 1912. It was also introduced to northern Tasmania in 1905, and has subsequently spread to the south and east of that island. During 1866 to 1880, a number of Laughing Kookaburras were released in New Zealand. Most of these failed to survive, but there are still small populations in North Island, where a few remain in Northland and on the western shore of Hauraki Gulf. Introductions were also made to Fiji prior to 1926, but the birds failed to establish themselves there.

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There can be little argument that the Tuamotu Kingfisher is rightly classified as a Vulnerable species. Its tiny range, covering the mere 26 km<sup>2</sup> of the island of Niau, in the Tuamotu Archipelago, holds a total population of some 400-600 individuals; the chance introduction of alien species could eliminate the kingfisher altogether. The nominate race of this species, from the Gambier Islands to the south, became extinct in the first quarter of the twentieth century. The possibility of translocating some individuals from Niau to other islands is being considered.

[*Todiramphus gambieri gertrudae*,  
Tuamotu,  
French Polynesia.  
Photo: Roland Seitre/  
BIOS]







## Subfamily HALCYONINAE

Genus *ACTENOIDES* Bonaparte, 1850

## 1. Green-backed Kingfisher

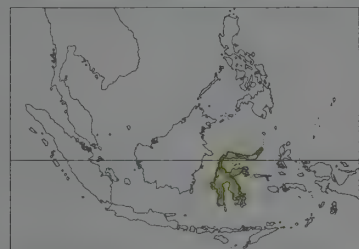
*Actenoides monachus*

**French:** Martin-chasseur moine      **German:** Einsiedlerliest      **Spanish:** Alción Monje  
**Other common names:** Blue-headed/Celebes Green/Celebes Lowland/Celebean Blue-and-white/Cowled/Lonely/Lowland Kingfisher, Blue-headed Wood Kingfisher

**Taxonomy.** *Halcyon* (*Paralcyon*) *monachus* Bonaparte, 1850, Sulawesi. Genus sometimes merged into *Halcyon*; alternatively, present species occasionally separated in monospecific genus *Dacelacyon*. Population of NC Sulawesi, formerly separated as race *intermedius*, now considered inseparable from nominate *monachus*. Two subspecies currently recognized.

**Subspecies and Distribution.**

*A. m. monachus* (Bonaparte, 1850) - N & C Sulawesi, including islands of Manadotua and Lembah. *A. m. capucinus* (A. B. Meyer & Wilesworth, 1896) - E, SE & S Sulawesi.



**Descriptive notes.** 31-32 cm. Large, heavy kingfisher with green back and wings, rufous collar, and rufous underparts apart from white throat. Male nominate race head blue, tail bluish-green; bill bright red; iris brown; legs and feet orange-red. Female like male, but ear-coverts and cheeks dark chestnut, forehead and superciliary stripe orange-rufous. Juvenile like female, but duller underparts, bill dusky with pale tip. Race *capucinus* black head, no blue on tail. **VOICE.** Long, melodious, ascending and descending whistles, repeated at intervals of 6 seconds; also shorter (2 seconds), slowly rising "huhuu", after a slight break a mournful

higher-pitched "wéééé", and ending with brief subdued, lower "uu", repeated at intervals of 6 seconds; calls mainly around dawn, also later in day if overcast; harsh "raak-raak-kraaa" alarm.

**Habitat.** Dense lowland forest and tall secondary forest, at up to 900 m. Replaced by *A. princeps* at higher altitudes.

**Food and Feeding.** Large centipedes (Chilopoda) and beetles (Coleoptera). Sits quietly in understorey or in middle storey, 1-5 m above ground, often close to a tree trunk or on a fallen trunk, then pouncing on prey in leaf litter. May be partly crepuscular.

**Breeding.** Little known. Probably lays in Feb-Mar; recently fledged young recorded in Apr. Nest with eggs found in Mar, in hole dug into arboreal termitarium; tunnel was 5 cm in diameter, 23 cm long, ending in nest-chamber 15 cm in diameter. No other information.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Restricted-range species; present in Sulawesi EBA. Generally uncommon, but locally common in N; present in Lore Lindu National Park, Dumoga-Bone National Park and Tangkoko DuaSudara Nature Reserve. Population has almost certainly declined in recent decades as result of extensive forest destruction. Continuing clearing of lowland forest for agriculture and logging could render species vulnerable.

**Bibliography.** Andrew (1992), Anon. (1996), van den Berg & Bosman (1986), Catterall (1997), Coates & Bishop (1997), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Holmes & Philipps (1996), Inskipp *et al.* (1996), Jepson (1997), Knowles & Nitcher (1995), Robson (1992), Rozendaal & Dekker (1989), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Stresemann (1940), Sujatnika *et al.* (1995), Watling (1983), White & Bruce (1986).

## 2. Scaly-breasted Kingfisher

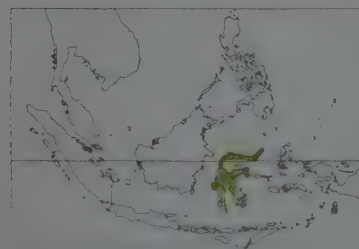
*Actenoides princeps*

**French:** Martin-chasseur royal      **German:** Königsliest      **Spanish:** Alción Real  
**Other common names:** Regent/Princely/Celebes Mountain/Scaly/Montane Kingfisher, Bar-headed Wood Kingfisher

**Taxonomy.** *Monachalcyon princeps* Reichenbach, 1851, Sulawesi. Genus sometimes merged into *Halcyon*; alternatively, present species occasionally separated in monospecific genus *Monachalcyon*. Three subspecies recognized.

**Subspecies and Distribution.**

*A. p. princeps* (Reichenbach, 1851) - NE Sulawesi.  
*A. p. erythrorhamphus* (Stresemann, 1931) - NW, C & SW Sulawesi.  
*A. p. regalis* (Stresemann, 1932) - SE Sulawesi.



**Descriptive notes.** 24-25 cm. Male of nominate race has blue head, buff- to rufous-tinged collar, and brown back with buff scallops; pale underparts with fine barring; bill yellowish-brown; iris dark brown; legs and feet yellowish-brown. Female like male, but buffy eyebrow and moustache. Juvenile like female, but more extensive rufous barring on back, bill dark brown with pale tip. Race *erythrorhamphus* red bill, more rufous collar and underparts; *regalis* (male unknown) distinctive, greenish crown, rump and primaries, unbarred back, almost plain rufous below. **VOICE.** Single mournful whistle that rises and falls; also series of soft mournful whistles, first rolling, then rising in pitch, then falling away; generally calls before dawn.

rising in pitch, then falling away; generally calls before dawn.

**Habitat.** Primary and tall secondary hill and montane forest, mainly at 900-2000 m, occasionally as low as 250 m. Seen chiefly in lower stratum of forest, but also in lower canopy. Largely separated altitudinally from *A. monachus*, which occurs at lower elevations, although some overlap exists.

**Food and Feeding.** Few data available. Insects, beetles (Coleoptera), also cicada (Cicadidae) nymphs known to be taken.

**Breeding.** Little known. Reported to make nesting tunnel in earth bank; clutch of 4 eggs collected. **Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Restricted-range species; present in Sulawesi EBA. Reportedly uncommon, but this may reflect its shy, inconspicuous habits. Present in Lore Lindu National Park and in Tangkoko DuaSudara Nature Reserve. May be threatened by forest clearing.

**Bibliography.** Andrew (1992), Anon. (1996), Coates & Bishop (1997), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Holmes & Philipps (1996), Inskipp *et al.* (1996), Jepson (1997), Knowles & Nitcher (1995), Rozendaal & Dekker (1989), Stattersfield *et al.* (1998), Stresemann (1940), Sujatnika *et al.* (1995), Watling (1983), White & Bruce (1986).

## 3. Moustached Kingfisher

*Actenoides bougainvillei*

**French:** Martin-chasseur à moustaches      **German:** Bartliest      **Spanish:** Alción Bigotudo

**Taxonomy.** *Halcyon bougainvillei* Rothschild, 1904, Bougainville Island.

Genus sometimes merged into *Halcyon*. Present species geographically separated from congeners; may provide a link between *Actenoides* and *Tanyptera*. Two subspecies recognized.

**Subspecies and Distribution.**

*A. b. bougainvillei* (Rothschild, 1904) - Bougainville (N Solomons).  
*A. b. excelsus* (Mayr, 1941) - Guadalcanal (S Solomons).



**Descriptive notes.** 30-32 cm; female 160-215 g (*excelsus*). Large and distinctive, with orange-rufous head, mantle and underparts; purple-blue eyestripe meets across nape; moustache, wings and tail all purple-blue; pale blue rump; red bill. Male nominate race purple-blue back, scapulars and tertials; iris dark brown; legs and feet red. Female similar, but olive-green lower back, scapulars and tertials. Juvenile undescribed. Race *excelsus* adult male undescribed; female more extensive green on back and paler underparts than nominate female; immature male very dark olive-green on back, scapulars and tertials. **VOICE.** Loud, ringing laugh, "ko, ko, ko,

ko, ko, ..."; possibly calls only in the periods just prior to dawn and after dusk.

**Habitat.** Lowland and hill forest on Bougainville; hill forest and mistforest, at 550-1550 m, on Guadalcanal. In 1994 and 1997, on Guadalcanal, heard calling only from patches of closed-canopy montane rainforest between 1000 m and 1550 m, but not in secondary forest on landslips, nor in open forest on very steep slopes, nor in mistforest at highest altitudes.

**Food and Feeding.** Little information. Stick-insects (Phasmida) and frogs taken.

**Breeding.** Females with somewhat developed ovaries collected in Jul on Guadalcanal. No detailed information. Said to nest in hole in riverbank, or in ground in forest; nest reported in arboreal ant nest on Bougainville. No other data.

**Movements.** Unknown; presumably sedentary.

**Status and Conservation.** VULNERABLE. Restricted-range species; present in Solomon Group EBA. Rare and restricted in both distribution and habitat. Crepuscular, possibly even nocturnal, habits, however, make it easily overlooked, but has a distinctive and far-carrying call. Total population estimated at between 250 and 1000 individuals. Has not been reliably reported from Bougainville since 1930's, though calls said to have been heard there in 1986 and pair reportedly seen at nest-hole in late 1980's; further corroborative evidence needed, but this island has been off-limits to ornithologists for many years. Reports from Guadalcanal since 1994 suggest that this species is locally common in suitable habitat, but recorded in recent years only from one small site there. On Bougainville, may occur at altitudes where forest is threatened by logging; on Guadalcanal, occurs at altitudes above areas of human activity, although much suitable habitat is lost through natural landslips. As a hole-nesting species, it is potentially threatened by introduced rats and cats.

**Bibliography.** Bishop (1987), Cain & Galbraith (1956), Coates (1985), Collar & Andrew (1988), Collar *et al.* (1994), Diamond (1987), Doughty *et al.* (1999), Dutton (2000), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Galbraith & Galbraith (1962), Gibbs (1996), Gregory (2000), Hadden (1981), Knowles & Nitcher (1995), Mayr (1945), Mountfort (1988), duPont & Niles (1980), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Tomlinson (2000).

## 4. Blue-capped Kingfisher

*Actenoides hombroni*

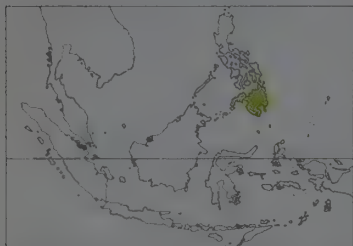
**French:** Martin-chasseur de Hombron      **German:** Mindanaoliest      **Spanish:** Alción de Mindanao  
**Other common names:** Hombron's Kingfisher/Wood Kingfisher

**Taxonomy.** *Actenoides hombroni* Bonaparte, 1850, Oceania; error = Philipines.

Genus sometimes merged into *Halcyon*. Forms a superspecies with *A. lindsayi* and *A. concretus*, and all sometimes regarded as conspecific. Birds from E Mindanao, described as race *burtoni*, poorly differentiated from those in rest of range and not considered worthy of subspecific recognition. Monotypic.

**Distribution.** Mindanao (SW Philipines).

**Descriptive notes.** 27 cm; male 108-124 g, female 106-147 g. Male has dark purple-blue crown and moustache, rufous ear-coverts; green-blue back and upperwing-coverts with small buff spots, blue rump, dark purple-blue tail; white chin and throat (sometimes more rufous in E populations), rufous underparts; bill red, becoming brownish-black on culmen; iris dark brown; legs and feet olive-brown to orange-flesh. Female has crown and moustache duller and greener, back and upperwing-coverts olive-green with buff spots, tail greenish-blue. Juvenile duller than adult. **VOICE.** Main call



rapid stuttering trill of 4-8 notes, followed by longer, more spaced pulsed notes; short, loud disyllabic "te-u" or "ki-aw" at 3-second intervals, often in duet; screeching "kaaa-a-a-a" at c. 1-second intervals also recorded.

**Habitat.** Undisturbed rainforest, and montane and mossy forest, occasionally secondary forest or disturbed habitats, in hilly areas; at 800-2400 m, mostly above 1000 m, rarely down to 100 m.

**Food and Feeding.** Large insects, including grasshoppers and locusts (Orthoptera), beetles and their larvae (Coleoptera), also snails (Gastropoda), frogs and small reptiles; apparently, fish also taken on occasion. Perches in lower storey, and probably flies to ground to catch its prey.

**Breeding.** Individuals with enlarged gonads suggest breeding in Mar-May; dates when juveniles observed indicate season possibly Jan-Jul. Nest, eggs and other aspects of breeding undocumented. **Movements.** Presumably sedentary.

**Status and Conservation.** **VULNERABLE.** Restricted-range species; present in Mindanao and the Eastern Visayas EBA. Since 1980 recorded from only 7 localities, 4 in C portion of the island and 3 in E. Present in Mt Kitanglad Natural Park, Mt Malindang National Park and Mt Matutum Forest Reserve; may still occur in Mt Apo Natural Park, although that has suffered massive human encroachment; pre-1970 records exist from watershed reserve at Mt Hilong-hilong, and possibly still occurs there. Difficult to observe and easily overlooked, but this species' call remained unknown until recently; since then, found to be fairly common in late 1990's at L Sebu, in S Mindanao, and may prove to be commoner than suspected elsewhere. Total population estimated at up to 10,000 individuals, but declining rapidly. Largely restricted to primary montane forest, where appears very rare and its habitat much reduced and fragmented. Main threats are continuing deforestation, especially at elevations below c. 1200 m, and mining activities; on Zamboanga Peninsula, in W, burning of forest an additional problem. Information on its biology is urgently required.

**Bibliography.** Anon. (1994a, 1997a), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Mallari & Tabaranza (1999), Delacour & Mayr (1946), Dickinson *et al.* (1991), Evans, Dutton & Brooks (1993), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Hachisuka (1933), Inskipp *et al.* (1996), Kennedy *et al.* (2000), Knowles & Nitcher (1995), Mountfort (1988), duPont (1971, 1976a), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Tomlinson (2000).

## 5. Spotted Kingfisher

### *Actenoides lindsayi*

**French:** Martin-chasseur tacheté **German:** Tropfenliet **Spanish:** Alción Moteado  
**Other common names:** Spotted Wood Kingfisher

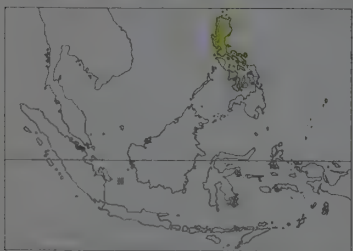
**Taxonomy.** *Dacelo Lindsayi* Vigors, 1831, Manila, Philippines.

Genus sometimes merged into *Halcyon*. Forms a superspecies with *A. hombroni* and *A. concretus*, and all three sometimes regarded as conspecific. Two subspecies recognized.

**Subspecies and Distribution.**

*A. l. lindsayi* (Vigors, 1831) - Luzon, Marinduque and Catanduanes (N Philippines).

*A. l. moseleyi* Steere, 1890 - Panay and Negros (C Philippines).



**Descriptive notes.** 26 cm. Distinctive, with buff spotting above and scallops below. Male of nominate race has dark green crown with black spots, light green stripe above pale blue supercilium, black eyeband, rufous lores, cheeks, collar and throat with prominent blue moustache; olive-green upperparts with prominent buff spots, plain green rump; whitish below, large green scallop marks on breast and flanks; upper mandible black with thin yellow central line, lower orange-yellow; iris dark brown; legs and feet greenish-flesh. Female has crown less dark green, lores yellow, cheeks and throat whiter, moustache green. Juvenile

generally duller, bill grey with yellow tip and base. Race *moseleyi* darker and browner above, buff spots somewhat larger and more rounded. **VOICE.** Main call explosive, stuttering trill 1 second long on ascending scale, "tu-tu-tu-tu", followed by 5 or 6 descending drawn-out notes each of c. 0.4 seconds, whole series c. 6-9 seconds long; also loud whistled "ptuuoo" 0.8 seconds long, given before dawn, and often preceding the main call; rasping chatter in alarm.

**Habitat.** Primary and secondary lowland and hill rainforest, sometimes near forest streams; generally below 1200 m. On Negros, has also been recorded in dense scrub in gardens.

**Food and Feeding.** Insects, beetles (Coleoptera) and snails (Gastropoda), also some small vertebrates. Perches low down in dark areas of forest; probably takes its prey from the ground.

**Breeding.** Birds with enlarged gonads and females with eggs in oviduct recorded in Mar, Apr and May. Thought to dig nest-hole in arboreal termite nest. No other information.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. No details available on population sizes. Unobtrusive and easily overlooked; reported as rare on Luzon. Appears to be virtually restricted to forest, a habitat which has been greatly reduced and fragmented by clearing and logging; although it seems able to withstand a certain degree of habitat disturbance, this species could become threatened in the future. Information on its biology is urgently required.

**Bibliography.** Brooks *et al.* (1992), Danielsen *et al.* (1994), Delacour & Mayr (1946), Dickinson *et al.* (1991), Evans, Dutton & Brooks (1993), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Gilliard (1950a), Gonzales & Rees (1988), Goodman & Gonzales (1990), Inskipp *et al.* (1996), Kennedy *et al.* (2000), Knowles & Nitcher (1995), duPont (1971), Poulsen (1995), Whitehead (1899).

## 6. Rufous-collared Kingfisher

### *Actenoides concretus*

**French:** Martin-chasseur trapu **German:** Malaienliet **Spanish:** Alción Malayo  
**Other common names:** Chestnut-collared Kingfisher

**Taxonomy.** *Dacelo concreta* Temminck, 1825, Sumatra.

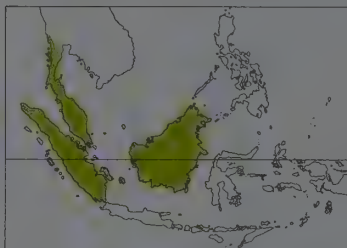
Genus sometimes merged into *Halcyon*. Forms a superspecies with *A. hombroni* and *A. lindsayi*, and all three sometimes considered conspecific. Three subspecies recognized.

**Subspecies and Distribution.**

*A. c. peristephes* (Deignan, 1946) - S Myanmar (S Tenasserim) and peninsular Thailand (Trang).

*A. c. concretus* (Temminck, 1825) - S peninsular Thailand (Trang) S to Sumatra, including Mentawai Is, Bangka and Belitung.

*A. c. borneanus* (Chasen & Kloss, 1930) - Borneo.



**Descriptive notes.** 23-24 cm; male 62-89 g, female 60-90 g. Solid, medium-sized kingfisher. Male nominate race green cap, light blue hindcrown, black eyeband and band across nape, rufous collar, yellow-buff supraloral line and cheeks, dark blue moustache; dark blue back, wings and tail, lighter blue rump; buff chin and throat, rufous breast and flanks, paler on belly; bill yellow, with black on culmen; iris dark brown; legs and feet pale yellow-green. Female back and wings dark olive-green with buff spots, bill duller. Juvenile like duller adult, male with spotted back, scapulars and wing-coverts, bill grey-brown with tip and base

of lower mandible yellowish. Race *peristephes* larger, collar and underparts paler, female large buff wing spots; *borneanus* darker upperparts, female more prominent spots. **VOICE.** Call loud, rising, repeated whistle, "kwee-i", at 1 per second, or singly at much longer intervals; also softer, more tremulous whistle, and low chuckling noises.

**Habitat.** Evergreen to semi-evergreen dense lowland forest, also forest regenerated to closed-canopy stage; montane and hill forest to 1200 m in Thai-Malay Peninsula, but in Borneo to 1700 m on Mt Kinabalu, where probably more common at the higher levels. Found in understorey to middle stratum of forest.

**Food and Feeding.** Invertebrates, including Isopoda, cicadas (Cicadidae), longicorn beetles (Cerambycidae), mantises (Mantodea), spiders, scorpions to 9 cm long, and snails (Gastropoda); also vertebrates, including small fish, snakes (*Doliophis*, *Maticora*, *Typhlops*) and lizards. Perches low in the forest and surveys ground and foliage for prey, with slow tail-wagging and head-cocking; will also perch over rivers, swooping down to catch food. Sometimes displaces leaf litter to reveal prey. May be able to remove the stings of scorpions.

**Breeding.** Lays in Mar in Sumatra, in Apr-Jun in Malaysia, and in Dec-Mar in Borneo. Nest-burrow in low bank, usually near a stream, sometimes in rotten tree trunk, or in sloping ground on forest floor 16-70 m from water; tunnel 10 cm in diameter, 60 cm long, ending in nest-chamber 20 cm in diameter. Clutch 2 eggs; nestling period c. 22 days. A ringed male survived over 20 years.

**Movements.** Sedentary. In Malay Peninsula, an individual was repeatedly recaptured at same site for over 4 years, another in Borneo (Sarawak) for 29 months.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Extinct in Singapore for at least 40 years, probably much longer. In Pasoh research area, in Negeri Sembilan (S Peninsular Malaysia), minimum density of 1 pair/5 ha of mature lowland forest and 1 pair/8 ha of regenerating lowland forest. Habitat reduction and fragmentation caused by logging are reducing its range, but its presence in hill forest means that it is under less threat than species confined to lowland forest; thought unlikely to remain in areas where logging activities lead to disruption of forest canopy. More information on its biology is required.

**Bibliography.** Andrew (1992), Burton (1978b), Chasen & Hoogerwerf (1941), Gibson-Hill (1949a, 1949b), Gore (1968), Inskipp *et al.* (1996), Jeyarajasingam & Pearson (1999), Lekagul & Round (1991), MacKinnon & Philipps (1993), van Marle & Voous (1988), McClure (1998), Medway & Nisbet (1967), Medway & Wells (1976), Mees (1986), Meyer de Schauensee & Ripley (1940), Robson (2000a), Round (1988, 1992), Smythies (1986, 1999), Stattersfield & Capper (2000), Thompson (1966), Verheugt *et al.* (1993), Wells (1985, 1999).









# Genus *TANYSIPTERA* Vigors, 1825

## 7. Common Paradise-kingfisher

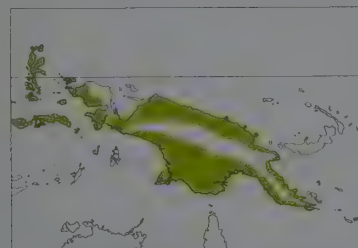
### *Tanysiptera galatea*

**French:** Martin-chasseur à longs brins **German:** Spatelliest **Spanish:** Alción Colilargo Común  
**Other common names:** Galatea Racquet-tail; Rossel Island Racquet-tail (*rosseliana*)

**Taxonomy.** *Tanysiptera galatea* G. R. Gray, 1859, Manokwari, New Guinea. Forms a superspecies with *T. ellioti*, *T. riedelii* and *T. carolinae*; commonly regarded as conspecific with the first two, but morphological differences, combined with geographical isolation, support treatment as separate species. Fifteen subspecies currently recognized.

#### Subspecies and Distribution.

- T. g. brunhildae* Jany, 1955 - Doi I, off N Halmahera (N Moluccas).
- T. g. emiliae* Sharpe, 1871 - Rau I, off N Halmahera.
- T. g. doris* Wallace, 1862 - Morotai.
- T. g. browni* Ripley, 1983 - Halmahera.
- T. g. sabrina* G. R. Gray, 1860 - Kayoa I, off SW Halmahera.
- T. g. margarethae* Heine, 1859 - Bacan.
- T. g. obiensis* Salvadori, 1877 - Bisa, Obi Latu and Obi.
- T. g. acis* Wallace, 1863 - Buru.
- T. g. boanensis* Mees, 1964 - Boano I, off NW Seram.
- T. g. nais* G. R. Gray, 1860 - Manipa, Ambon, Seram, Manawoka and Gorong.
- T. g. galatea* G. R. Gray, 1859 - W Papuan Is. E to Geelvink and Triton Bays.
- T. g. meyeri* Salvadori, 1889 - N New Guinea.
- T. g. vulcani* Rothschild & Hartert, 1915 - Manam I, off NE New Guinea.
- T. g. minor* Salvadori & D'Albertis, 1875 - S New Guinea.
- T. g. rosseliana* Tristram, 1889 - Rossel I, in Louisiade Archipelago.



**Descriptive notes.** 33-43 cm, including tail-streamers; male 58-65 g, female 55-69 g (*galatea*), 40-78 g (other races). Male nominate race blue crown, dark blue upperparts, white rump; bluish-white outer tail, central rectrices up to 20 cm longer than rest, blue with white spatulate tips; underparts white; bill red; iris dark brown; legs and feet brownish-grey to yellow-brown. Differs from very similar *T. hydrocharis* in slightly larger size, paler crown, whitish outer tail. Female like male, but slightly smaller. Juvenile brown upperparts, rich blue edges to crown feathers, yellowish-buff below, breast rufous with darker margins giving scalloped appearance, brown bill. Races vary mainly in depth of colour of crown and wing-coverts, amount of white in tail, colour of upper back and rump: *margarethae* distinctive, rump feathers broadly edged blue, tail mostly blue; *emiliae*, *doris* and *sabrina* white on upper back; *vulcani* and *rosseliana* tail mostly white. **VOICE.** 1-4 mournful whistles, at same pitch, accelerating to a trill, lasting 1.5 seconds; several birds may sing together, tail jerked high as they call; other calls include low, mournful whistle, "wheeyou", downslurred for 1.5 seconds, or upslurred and longer (2-3 seconds); also rasping chatters and shrill squawks.

**Habitat.** Monsoon forest and primary lowland rainforest, to 300 m, occasionally to 820 m. Also found in gallery forest along watercourses in grassy valleys, and in forest fragments in savanna, in secondary forest, and in old teak plantations. Presence of arboreal termitaria may be essential part of habitat. Absent or scarce in areas where *T. danae*, *T. nympha* or *T. sylvia* occur. Dispersing juveniles sometimes found in atypical habitats, such as dry savanna, parks, suburban gardens.

**Food and Feeding.** Many earthworms (Annelida) taken; also snails (Gastropoda), beetles (Coleoptera), grasshoppers (Orthoptera), caterpillars (Lepidoptera), centipedes (Chilopoda), and small lizards. Nestlings are fed mainly on earthworms, but also insects, lizards and armoured centipedes. Forages by sitting in dark forest understorey, swooping to ground for prey, which is carried back to the branch in bill, and beaten before being swallowed; will also snatch insects from foliage 1 m above ground. Foraging on ground more common in the wet season. Earthworms are taken from damp ground by digging and probing with bill; worm is dragged out and carried to a perch, where beaten and worked in bill before being swallowed.

**Breeding.** Lays in wet season, Oct-Mar (Jul) in Papua New Guinea. Nest 2-6 m above the ground in arboreal termitarium of *Microcerotermes biroi*, tunnel excavated by both sexes, and many attempts made before a suitable termitarium selected; one tunnel was 15 cm long, with nesting chamber 13 cm in diameter; reported nest-sites in tree hollows and earth banks require confirmation. Clutch of 5 eggs recorded, and 5 recently fledged young seen together; both sexes feed the young. Breeding success high, juveniles comprising 60% of population at end of wet season, but juvenile mortality also high. Longevity over 5 years in favourable areas.

**Movements.** Generally very sedentary, adults maintaining a territory throughout year and moving little more than 100 m over several years; young birds disperse several km from parental territory. Vacates monsoon forest, however, in dry season. Vagrant reported from Darnley I, in Torres Strait.

**Status and Conservation.** Not globally threatened. In some areas, can be very numerous, with densities of e.g. 5 birds/ha, and, locally, individuals can live for fairly long time. On other hand, habitat reduction and fragmentation is reducing its range, and this may be serious problem for some island subspecies.

**Bibliography.** Andrew (1992), Bailey (1992), Bechler (1978), Bechler *et al.* (1986), Bell (1971, 1980, 1982a), Bowler & Taylor (1989), Coates (1969, 1985), Coates & Bishop (1997), Diamond (1972), Draffan (1978), Finch (1981b), Fletcher (2000b), Garnett & Smith (1997), Gilliard & LeCroy (1966), Greenway (1966), Gyldestolpe (1955b), Hartert (1903), Heinrich (1956), Higgins (1999), Hoogerwerf (1971), Inskipp *et al.* (1996), Iredale (1956), Isherwood *et al.* (1997), Johnson & Stattersfield (1990), Mackay (1970), Mayr & Rand (1937), Mees (1982), Pearson (1975b), Peckover & Filewood (1976), Ramsay (1879), Rand & Gilliard (1967), Ripley (1964, 1983), Simpson & Day (1998), Tomlinson (2000), Varghese (1977), Weston (1975), White & Bruce (1986).

## 8. Kofiau Paradise-kingfisher

### *Tanysiptera ellioti*

**French:** Martin-chasseur de Kofiau **German:** Elliottiest **Spanish:** Alción Colilargo de la Kofiau  
**Other common names:** Elliot's Paradise-kingfisher/Racquet-tail

**Taxonomy.** *Tanysiptera ellioti* Sharpe, 1870, no locality = Kofiau Island. Forms a superspecies with *T. galatea*, *T. riedelii* and *T. carolinae*; commonly regarded as conspecific with the first two, but morphological differences, combined with geographical isolation, support treatment as separate species. Monotypic.

**Distribution.** Kofiau I (W Papuan Is.).



**Descriptive notes.** 33-34 cm, including tail-streamers. Both sexes blue crown, dark blue upperparts, white rump and underparts; tail white, central rectrices slightly tapered, 10-11 cm longer than rest of tail; bill red; iris dark brown; legs and feet brown-grey to yellow-brown. Differs from very similar *T. galatea* in entirely white tail, long central tail feathers narrowing only slightly and with less marked spatulate tips. Juvenile duller than adult, wing-coverts edged with buff, lower back and rump washed with pale brown, underparts washed with brownish-buff, short tail blue above and grey below, bill dusky brown with paler tip. **VOICE.** Undescribed.

**Habitat.** Primary and tall secondary forest.

**Food and Feeding.** No information; individuals with heavily worn breast feathers suggest foraging for insects in muddy forest understorey.

**Breeding.** No information.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Data-deficient. Restricted-range species: present in West Papuan Lowlands EBA. Very little-known species. Reported as common and widespread in "most" habitats in the lowlands, but no numerical data available. Although seems to be tolerant of selective logging, status of forest habitats in Kofiau, which has no protected areas, is poorly known; species may be declining.

**Bibliography.** Andrew (1992), Bechler *et al.* (1986), Coates (1985), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Iredale (1956), Knowles & Nitchen (1995), Rand & Gilliard (1967), Ripley (1959a, 1964), Stattersfield *et al.* (1998).

## 9. Biak Paradise-kingfisher

### *Tanysiptera riedelii*

**French:** Martin-chasseur de Biak **German:** Biakliet **Spanish:** Alción Colilargo de la Biak  
**Other common names:** Riedel's Racquet-tail

**Taxonomy.** *Tanysiptera Riedelii* J. Verreaux, 1866, no locality = Biak Island. Forms a superspecies with *T. galatea*, *T. ellioti* and *T. carolinae*; commonly regarded as conspecific with the first two, but morphological differences, combined with geographical isolation, support treatment as separate species. Monotypic.

**Distribution.** Biak I and adjoining Supiori I, in Geelvink Bay (NW New Guinea).



**Descriptive notes.** 37 cm, including tail-streamers; male 63-70 g, female 55-72 g. Both sexes brilliant pale blue crown and nape, dark blue upperparts, white rump and tail; central rectrices 15-16 cm longer than rest, white at base, blue in narrow central portion, with white spatulate tips; white underparts; bill orange-red; iris dark brown; legs and feet greenish-grey to yellowish-brown. Distinguished from similar *T. galatea* by brighter blue crown and nape, more white in tail, stouter bill. Juvenile duller upperparts, shorter tail pale buff and scalloped, dusky brown bill. **VOICE.** Low, distinctive, barking call of 1 or 2 notes.

**Habitat.** Dense primary forest, particularly bordering watercourses, possibly also secondary and disturbed forest; to at least 300 m, possibly to 600 m.

**Food and Feeding.** No information; presumably similar to other *Tanysiptera* species.

**Breeding.** No information.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Restricted-range species: present in Geelvink Islands EBA. Occurs in the Biak-Urara Protected Area, which covers 110 km². Poorly known, and conflicting reports on its abundance; alleged to be fairly common in primary, secondary and logged forest, but reported by others to be rare and to be restricted to tall forest. Although forest habitat on Biak seriously threatened from logging and subsistence farming, there appear to be large areas of forest remaining on Supiori. If species is able to tolerate degraded forest, as some reports suggest, then it may survive without too many problems; its adaptability and its present population level are uncertain, however, and further research may show that it is under threat.

**Bibliography.** Andrew (1992), Bechler *et al.* (1986), Coates (1985), Collar & Andrew (1988), Eastwood (1996), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Iredale (1956), Knowles & Nitchen (1995), Mayr & Meyer de Schauensee (1939), Mountfort (1988), Rand & Gilliard (1967), Stattersfield *et al.* (1998), Sujatnika *et al.* (1995).

## 10. Numfor Paradise-kingfisher

### *Tanysiptera carolinae*

**French:** Martin-chasseur de Caroline **German:** Numforliet **Spanish:** Alción Colilargo de la Numfor  
**Other common names:** Caroline Racquet-tail



**Taxonomy.** *Tanysiptera Carolinae* Schlegel, 1871, Numfor Island.  
Forms a superspecies with *T. galatea*, *T. ellioti* and *T. riedelii*. Monotypic.  
**Distribution.** Numfor I, in Geelvink Bay (NW New Guinea).



**Descriptive notes.** 34-38 cm, including tail-streamers. Unmistakable. Both sexes purple-blue upperparts and underparts, except for white lower back, rump, tail and vent; central rectrices extending 7-8 cm beyond others; blue shafts with white spatulate tips; bill red; iris dark brown; legs and feet dusky brown. Juvenile dark blue above with white rump, but dark tail, rufous underparts, dusky brown bill. **VOICE.** Described as similar to that of the Common Cuckoo (*Cuculus canorus*) but louder. **Habitat.** Lowland forest, open woodland and farmland, also beach vegetation.

**Food and Feeding.** Grasshoppers (Orthoptera),

large beetles (Coleoptera), and snails (Gastropoda).

**Breeding.** Reported to nest in termitaria. No other information.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Restricted-range species: present in Geelvink Islands EBA. Common and widespread in all lowland habitats on Numfor I. Logging and subsistence farming have already led to the destruction or degradation of much of the forest on Numfor, an island with a surface area of only 330 km<sup>2</sup>. No protected areas currently exist there, but there are proposals for a reserve. Although this species appears to be adaptable, and able to survive well in highly degraded forest and marginal habitats, its ecological requirements remain poorly known; also, little is known about the current condition of forest on the island. Further research needed on these aspects, as well as information on the species' biology and present numerical status.

**Bibliography.** Andrew (1992), Beehler *et al.* (1986), Bleiweiss (1987), Coates (1985), Collar & Andrew (1988), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Iredale (1956), Knowles & Nitehen (1995), Rand & Gilliard (1967), Rothschild *et al.* (1932), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Sujatnika *et al.* (1995).

## 11. Aru Paradise-kingfisher

### *Tanysiptera hydrocharis*

**French:** Martin-chasseur menu **German:** Feenliest **Spanish:** Alción Colilargo de las Aru  
**Other common names:** Lesser/Little/Blue-tailed Paradise-kingfisher, Aru Island Racquet-tail

**Taxonomy.** *Tanysiptera hydrocharis* G. R. Gray, 1858, Aru Islands.

Closely related to *T. galatea*, from which thought probably to have differentiated in Aru Is, later invading mainland New Guinea, where now sympatric with that species without hybridizing. Monotypic.

**Distribution.** Aru Is, and S New Guinea in Trans-Fly region (R Merauke N to R Fly and E to R Oriomo).



**Descriptive notes.** 30 cm, including tail-streamers. Both sexes dark blue crown and upperparts, white rump and underparts; tail dark blue, central rectrices 11 cm longer than rest and with white margins, spatulate tips; bill red; iris dark brown; legs and feet olive grey. Distinguished from very similar *T. galatea* by slightly smaller size, dark blue crown and outer tail feathers. Juvenile browner, underparts rufous-buff with darker stripes, bill brown with horn-coloured base of lower mandible. **VOICE.** Insufficient information; probably similar to that of *T. galatea*.

**Habitat.** Dense lowland rainforest, including

drier habitats than those used by *T. galatea*.

**Food and Feeding.** Insects and insect larvae, taken from foliage and on the ground.

**Breeding.** Laying in Aru Is in Apr, recently fledged bird in May. Reported to nest in arboreal termitaria. No other information.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Data-deficient. Restricted-range species: present in Trans-Fly EBA. In mainland New Guinea it is generally considered rare, but status there difficult to assess because of possible confusion with *T. galatea*. On Aru Is was reported as common in 1955, but no recent information available. Recent records only from the Trans-Fly north of Kiunga, where it is reported as uncommon to common. No indication that species tolerates degraded habitats. Further data required on its ecology, biology and population levels.

**Bibliography.** Andrew (1992), Beehler *et al.* (1986), Coates (1985), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Gregory (1997), Hoberoff (1988), Iredale (1956), Knowles & Nitehen (1995), Mayr & Rand (1937), Rand (1938, 1942a), Rand & Gilliard (1967), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Tomlinson (2000).

## 12. Buff-breasted Paradise-kingfisher

### *Tanysiptera sylvia*

**French:** Martin-chasseur sylvain **German:** Paradisliet **Spanish:** Alción Colilargo Silvia  
**Other common names:** Australian/Long-tailed/Racquet-tailed/Silver-tailed/White-tailed Paradise-kingfisher, Australian Racquet-tail; Black-headed Paradise-kingfisher (*nigriceps*)

**Taxonomy.** *Tanysiptera sylvia* Gould, 1850, Cape York Peninsula, Queensland.

Sometimes placed in monospecific genus *Uralcyon*. Race *nigriceps* (with *leucura*) sometimes treated as forming a separate species. Non-breeding visitors to New Guinea described as race *mira*, but inseparable from nominate. Four subspecies recognized.

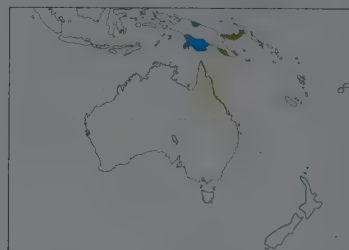
**Subspecies and Distribution**

*T. s. leucura* Neumann, 1915 - Umboi I (Bismarck Archipelago).

*T. s. nigriceps* P. L. Selater, 1877 - New Britain and Duke of York I.

*T. s. salvadoriana* E. P. Ramsay, 1879 - SE New Guinea, from R Angabunga to R Kemp Welch.

*T. s. sylvia* Gould, 1850 - NE Australia, from Cape York to Eurimbula; migrates to S & N New Guinea.



**Descriptive notes.** 29-37 cm, including tail-streamers; male 38-61 g, female 44-61 g. Both sexes nominate race blue head, blackish eyeband, dark blue upperparts with white spot on upper back, white rump; tail blue, white elongated central feathers remaining narrow to tip, 7-18 cm longer than rest of tail; underparts orange-buff; bill red; iris dark brown; legs and feet pink-red. Juvenile duller, bill brown. Race *salvadoriana* paler below; *nigriceps* black cap and scapulars, paler below, tail grey-blue except for white shafts, inner webs and tips of central feathers; *leucura* similar to last, but completely white

tail. **VOICE.** In Australia, piping call of 4-5 (up to 14) loud "chop" notes that become higher in pitch; soft downward-inflected trill given near nest, harsh, fast and loud when agitated; harsh screeching chatter in alarm and when driving off conspecifics; also soft coughs; young from 2 weeks old have very noisy rasping screeches. In E New Guinea, quiet rapid trill on one pitch, usually decelerating, also squawks, rattles, high-pitched "see", and shrill, descending series of 4 upslurred notes, "krei, krei, krei, krei". In New Britain, rising and falling series of chirps, accelerating to trill up to 7 seconds long.

**Habitat.** Monsoon forest, and lowland, notophyll vine and hill forest, usually with tall understorey and sparse ground cover; to 900 m in Australia and 1560 m in New Britain. Generally found near watercourses, and can be present in isolated patches of forest, but rarely in wet sclerophyll forest. Termite mounds an essential part of breeding habitat. In some areas sympatric with *T. galatea*, and then occupies higher levels of forest than latter; in other areas the two are mutually exclusive.

**Food and Feeding.** Wide variety of invertebrates, from beetles (Coleoptera), grasshoppers (Orthoptera), mantises (Mantodea), cockroaches (Blattodea), cicadas (Cicadidae), wasps and bees (Hymenoptera), and larvae, to centipedes (Chilopoda), spiders, earthworms (Oligochaeta) and snails (Gastropoda); also vertebrates, including frogs, tortoises (Pleurodira) and lizards (Scincidae). Snails have their shells removed by adults before being fed to nestlings. Prey taken from foliage in sally-hovers; also from the ground, where probably digs in the soil for earthworms and larvae.

**Breeding.** Laying dates in May, Jun and possibly Dec in New Britain, in Feb in mainland Papua New Guinea, and in Nov-Feb in Queensland. Nest excavated by both adults, generally in termitarium on ground but sometimes in arboreal one, but a nest-hole in New Britain was 5 m above ground in a tree, and a nest in Queensland was on a mound on a level streambank; in ground termitarium, nest-tunnel 13-17 cm above the ground, 4-5 cm wide and 13-20 cm long, ending in unlined nest-chamber 14 cm high and 17 cm wide; same nest-site may be used repeatedly for up to 8 years. Clutch usually 3 eggs (2-4), laid at 1-day intervals; both parents incubate, but only the female at night, incubation period 26-28 days; in Mackay (Queensland) study, only the female brooded the young, but both adults fed them, at rate of 1-6-12 feeding visits per hour; young squeak loudly in response to any stimulus; fledging period 26-35 days; juveniles fed by parents for 30 days after leaving nest. Goannas (*Varanus*) frequently raid nests, and are attacked by adults. Ringed individuals have lived at least 4 years.

**Movements.** Breeding populations in New Guinea and Bismarck Archipelago probably resident. Nominant race in Queensland migrates to New Guinea after breeding, although some occasionally remain in Australia; adults fly N in early Apr (Feb-May), and at Innisfail juveniles follow a few weeks later; return migration in early Nov; suggestions that populations on Cape York Peninsula arrive later than those breeding farther S, and that these two populations have different migratory routes, require confirmation.

**Status and Conservation.** Not globally threatened. Locally common in parts of its range, scarce or absent in others. Density of 8 pairs in 8 ha recorded at Innisfail, on NE Queensland coast, and a breeding pair stayed within territory of 0.33 ha; on Cape York Peninsula up to 5 nests/ha. Habitat loss is reducing some populations. Some birds of nominate race, while migrating at night, are killed by hitting lighthouses on the Great Barrier Reef or by flying into windows. Races *leucura* and *nigriceps* are common in lowland forest, including heavily degraded forest; although declining as a result of the large-scale deforestation on New Britain, they do not appear to be threatened.

**Bibliography.** Andrew (1992), Andrews (1993), Andrews & Brickhill (1991, 1995), Andrews *et al.* (1996), Barker & Vestjens (1989), Beehler *et al.* (1986), Bell (1982a), Berndsen (1990), Blakers *et al.* (1984), Boles (1984), Brickhill (1986), Clapp (1981), Coates (1985), Draffan *et al.* (1983), Dutton (2000), Eastman (1970), Eastwood & Hicks (1998), Gill (1964), Gilliard & LeCroy (1967a), Gregory (1995a), Hartert (1926), Higgins (1999), Iredale (1956), Kikkawa (1976), Lindsey (1992), Macdonald (1988), Mayr & Rand (1937), Nix (1984), Pizzey & Knight (1997), Rand & Gilliard (1967), Ripley (1964), Schodde & Tidemann (1986), Simpson & Day (1998), Sticklen & Sticklen (1981), Strahan (1994), Thomae (1974), Trounson & Trounson (1987), Weston (1975).

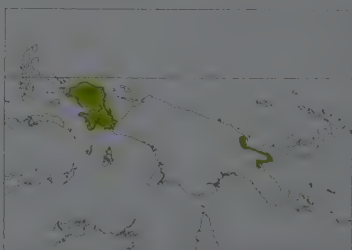
## 13. Red-breasted Paradise-kingfisher

### *Tanysiptera nympha*

**French:** Martin-chasseur nymphe **German:** Nymphenliet **Spanish:** Alción Colilargo Ninfa  
**Other common names:** Pink-breasted Paradise-kingfisher, Red-breasted Racquet-tail

**Taxonomy.** *Tanysiptera Nympha* G. R. Gray, 1840, New Guinea = Vogelkop Peninsula.

Forms a superspecies with *T. danae*. Proposed race *rothschildi* (Huon Peninsula) now considered invalid. Monotypic.



**Distribution.** New Guinea, in two disjunct populations: in W in Vogelkop Peninsula (E to Geelvink and Etna Bays), and in NE from Adelbert Mts E to Huon Peninsula and S to upper R Watut and Bulolo Valley.

**Descriptive notes.** 30-35 cm, including tail-streamers; male 57 g, female 47-57 g. Both sexes blue-black crown and upperparts, bright pink-red rump and underparts; tail purple-blue, elongated central feathers 8 cm longer than rest and with broad white tips and often with narrow white inner margins at base; bill orange-red; iris dark brown; legs and feet pink-orange to red. Differs from *T. danae* in having head

and upperparts blue, not brown. Juvenile brown upperparts, crown feathers edged with blue, pink-buff scalloped underparts, yellowish-orange bill darker at base. **VOICE.** 1-4 mournful whistles, becoming a trill; similar to that of *T. danae*.



**Habitat.** Lowland forest and ravines in forested hills, mainly below 900 m, occasionally up to 1500 m; also tall secondary growth and riverine and mangrove forest.

**Food and Feeding.** Insects, larvae, and possibly earthworms. Perches solitarily on low horizontal branches in understorey, scanning for prey.

**Breeding.** Undated clutch of 2 eggs from Huon Peninsula. No other information.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in West Papuan Lowlands EBA and North Papuan Lowlands EBA. Locally quite common, but has a small range and would be threatened by habitat clearance. Information required on its breeding biology.

**Bibliography.** Andrew (1992), Beehler (1978), Beehler *et al.* (1986), Coates (1985), Eastwood (1995a), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Hindwood (1959), Iredale (1956), Knowles & Nitchén (1995), Mayr & Rand (1937), Peckover & Filewood (1976), Rand & Gilliard (1967), Stattersfield *et al.* (1998), Sujatnika *et al.* (1995), Tomlinson (2000), Weston (1975).

**14. Brown-headed Paradise-kingfisher**

*Tanysiptera danae*

**French:** Martin-chasseur rose    **German:** Braunmantellist    **Spanish:** Alción Colilargo Dánae  
**Other common names:** Brown-backed Paradise-kingfisher, Ruddy Racquet-tail

**Taxonomy.** *Tanysiptera Danae* Sharpe, 1880, Milne Bay, New Guinea. Forms a superspecies with *T. nympha*. Proposed race *intensa* (named from W of Dyke Acland Bay) invalid. Monotypic.

**Distribution.** SE New Guinea, from R Waria and R Aroa E to Alotau.

**Descriptive notes.** 28-30 cm, including tail-streamers; male 37-46 g, female 42-50 g. Male rufous-brown crown and back, bright pink rump, blue wing-coverts; pink chin and throat, richer



deep pink breast and abdomen, paler flanks and undertail-coverts; purplish-blue uppertail, central feathers 9 cm longer than rest and with white tips and narrow inner margins at base, lateral tail feathers dusky grey; bill red; iris dark brown; legs and feet pink to orange-red. Female buff chin and throat. Juvenile browner crown, olive-brown upperparts, scaly underparts, orange bill with brown at base. **VOICE.** 1-4 mournful whistles accelerating to a trill, like that of *T. galatea* but quicker; also “wheeyou” call very like *T. galatea*.

**Habitat.** Found mainly in dense primary forest, most common between 500 m and 1000

m; also recorded from gallery and alluvium forest, and from *Castanopsis* forest, forest edges and secondary growth. This species and *T. galatea* seem to be mutually exclusive in some places, but elsewhere both occur together.

**Food and Feeding.** Insects, including beetles (Coleoptera) and caterpillars. Perches relatively higher in the forest than *T. galatea*.

**Breeding.** No information, but highest intensity of calling is from May to Oct.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Patchily distributed; scarce in some areas but common in others. Regularly recorded in Varirata National Park. No figures available on population levels, and no information on any possible threats. Data required on all aspects of its status and biology.

**Bibliography.** Beehler *et al.* (1986), Bell (1982a), Coates (1985), Eastwood & Thicks (1998), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Iredale (1956), Knowles & Nitchén (1995), Peckover & Filewood (1976), Rand & Gilliard (1967), Stattersfield *et al.* (1998), Weston (1975).



## PLATE 10

## Family ALCEDINIDAE (KINGFISHERS) SPECIES ACCOUNTS

### Genus *CITTURA* Kaup, 1848

#### 15. Lilac-cheeked Kingfisher

##### *Cittura cyanotis*

French: Martin-chasseur oreillard German: Blauohrliet Spanish: Martin Cazador de Célebes

**Other common names:** Blue-eared/Celebes/Sulawesi Blue-eared/Celebes Flat-billed Kingfisher, Lilac/Masked/Temminck's Kingfisher

**Taxonomy.** *Dacelo cyanotis* Temminck, 1824, Sumatra; error = Sulawesi. Distinctive, with no close relatives. Validity of race *modesta* has been questioned; may be inseparable from nominate. Three subspecies currently recognized.

##### **Subspecies and Distribution.**

*C. c. sanghirensis* Sharpe, 1868 - Sangihe Is (Sangihe, Siau), off N Sulawesi.  
*C. c. cyanotis* (Temminck, 1824) - N Sulawesi and Lembeh I.



*C. c. modesta* Stresemann, 1938 - SC & SE Sulawesi.



**Descriptive notes.** 28 cm. Distinctive, large forest kingfisher with brown crown, nape and back, purple-blue mask and upperwing-coverts, reddish-brown graduated tail. Male nominate race pale lilac ear-coverts of long, stiff feathers; chin, throat and breast very pale buff, suffused with lilac; bill, iris, legs and feet red. Female similar to male, but mask and upperwing-coverts black. Juvenile duller, bill grey-brown. Race *modesta* throat rufous-lilac, ear-coverts lilac in male, rufous in female; *sanghirensis* larger and brighter, forehead and malar region black, back more rufous, ear-coverts long, stiff and bright lilac, lilac-mauve

extending as a broad band across breast. **VOICE.** Very rapid "ku-ku-ku", repeated every few minutes; 3-4 descending, fairly high-pitched piping notes, starting with indistinct grace note, repeated at intervals of 2-3 seconds, sometimes answered by another individual. Race *sanghirensis* a slow, puppy-like "yap-yap", also a plaintive, quivering, nasal wail, and series of upslurred whistles.

**Habitat.** Primary and tall secondary lowland forest and drier hill forest, to 850 m on Sangihe and to 1000 m in Sulawesi; also mixed plantations of trees and crops. Observed to use bare branches of low trees for roosting.

**Food and Feeding.** Large insects, including mantises (Mantodea), cicadas (Cicadidae), grasshoppers (Orthoptera), leafhoppers (Cicadelloidea), and beetles (Cetoniinae); also millipedes (Diplopoda) and small reptiles. Sits quietly and almost motionless in dark lower and middle storeys of forest, or next to recently cleared land, often for protracted periods, scanning ground, and dives down to capture prey on the ground. Normally solitary.

**Breeding.** Little known. In mid-Oct, pair seen in forest at dawn, presumed male apparently displaying from horizontal perch 2 m above ground, slowly raised and fanned tail, the head also being raised, pointing bill up at sharp angle, while giving a grating trill lasting c. 4 seconds; display repeated 4 times in 2 minutes, before bird flew off. Nest in burrow, excavated in sloping ground. No other information.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Restricted-range species: present in Sulawesi EBA and Sangihe and Talaud EBA. Patchily distributed and generally uncommon in Sulawesi, but moderately common in N; relatively common in the Tangkoko-Batuangus Nature Reserve, and occurs in Dumoga-Bone National Park. Extensive clearing of forest has taken place on Sangihe, but still seems reasonably common there, where possibly more tolerant of secondary habitats than is Sulawesi population. Nevertheless, habitat destruction has been widespread within species' range and all populations have almost certainly suffered as a result. Further destruction of habitat is likely to be serious threat in many areas of its fragmented distribution. More information is urgently required on all aspects of its biology.

**Bibliography.** Andrew (1992), Anon. (1996), Aurivillius & Aurivillius (1993), Coates & Bishop (1997), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Gregory-Smith (1998), Holmes & Philipps (1996), Inskipp *et al.* (1996), Jepson (1997), Knowles & Nitcher (1995), Riley (1997a, 1997b, 1997c), Robson (1996b), Rozendaal & Dekker (1989), Sampiri (1996), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Stresemann (1940), Sujatnika *et al.* (1995), Wardill (1995, 1999), Wardill *et al.* (1999), Watling (1983), White & Bruce (1986).

## Genus **MELIDORA** Lesson, 1830

### 16. Hook-billed Kingfisher

#### *Melidora macrorrhina*

**French:** Martin-chasseur d'Euphrosine **German:** Hakenliest **Spanish:** Martin Cazador Ganchudo

**Taxonomy.** *Dacelo macrorrhinus* Lesson, 1827, Manokwari, New Guinea.

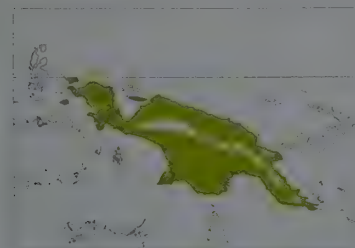
Although placed in monospecific genus, shows some similarities to *Tanyptera* and also to *Clytoceyx* and *Dacelo*. Three subspecies recognized.

**Subspecies and Distribution.**

*M. m. waigiuensis* Hartert, 1930 - Waigeo (W Papuan Is).

*M. m. macrorrhina* (Lesson, 1827) - Batanta, Salawati and Misool (W Papuan Is), and E across S & E New Guinea.

*M. m. jobiensis* Salvadori, 1880 - Yapen I, in Geelvink Bay, and E through N New Guinea to Astrolabe Bay.



**Descriptive notes.** 27 cm; male 90-110 g, female 85-110 g. Large, dumpy-looking kingfisher, black eyestripe and black band from chin joining at rear to form broad collar, bordered white below. Male of nominate race has broad blue or turquoise fringes to black crown feathers; upperparts and wing-coverts brown with buff tips; underparts whitish; large bill with black upper mandible, horn-coloured lower mandible, distinct hooked tip; iris very dark brown; legs and feet greenish-grey. Female yellowish-green fringes to forehead and crown, buffy underparts. Juvenile darker cap, underparts rufous-buff to yellowish-buff, noticeable

dusky margins to throat and breast feathers. Race *waigiuensis* slightly larger; *jobiensis* male deeper blue on crown, female blackish crown. **VOICE.** Calls mainly at dusk and dawn, but throughout night when moonlit, also by day when breeding, single liquid whistle, sometimes 2 or 3, followed by 1-4

short higher-pitched notes, "teuw-tu-tu", lasting c. 1 second; also 2 whistled notes, second shorter and higher; less frequently, irregular series of 3-5 plaintive notes, falling and rising, 2-5 seconds; repeated chatter in alarm and aggression.

**Habitat.** Lowland primary and secondary rainforest, gallery forest, scrub-forest, also partly cleared areas, isolated groups of trees, and older rubber and teak plantations; generally below 700 m, locally up to 1280 m.

**Food and Feeding.** Large insects, including stick-insects (Phasmida), also frogs. Feeding behaviour little known; bill often caked in mud, suggesting that it may dig in soil for prey. Mainly nocturnal or crepuscular, but forages actively during day when feeding chicks.

**Breeding.** Lays in middle to late dry season, in Jul-Oct. Nest dug into active termite nest 3-6 m above ground on side of a tree, in shady location; in one case, tunnel sloped up from side of termitarium to near top, where nest-chamber 11-12 cm wide was located. Clutch 2-3; hatching possibly asynchronous; male incubates and broods by day; nestling reported to have egg tooth on both upper and lower mandibles, and bill even more hooked than on adult; incubation and fledging periods not documented.

**Movements.** Sedentary; a ringed bird recovered 5-5 years later at same site.

**Status and Conservation.** Not globally threatened. Widely distributed and quite common. Occurs in Varirata National Park; fairly common in Kau Wildlife Area. Nocturnal habits means that it is infrequently seen, but up to 12 heard calling simultaneously in Baiyer River Sanctuary.

**Bibliography.** Andrew (1992), Bailey (1992), Beehler (1978), Beehler *et al.* (1986), Bell (1982a, 1986), Coates (1985), Diamond (1972), Eastwood (1995a), Finch (1980a), Fletcher (2000b), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Gilliard & LeCroy (1968), Gregory (1995a), Gyldestolpe (1955b), Hartert (1930), Hiaso *et al.* (1994), Iredale (1956), Knowles & Nitcher (1995), Mackay (1980, 1991), Mayr & Rand (1937), Mees (1965), Ramsay (1879), Rand (1942a, 1942b), Rand & Gilliard (1967), Safford & Smart (1995), Schodde & Hitchcock (1968).

## Genus **CLYTOCEYX** Sharpe, 1880

### 17. Shovel-billed Kingfisher

#### *Clytoceyx rex*

**French:** Martin-chasseur bec-en-cuillère

**German:** Frochschnabelliist

**Spanish:** Martin Cazador Picopala

**Other common names:** Shovel-billed Kookaburra, Emperor/Crab-eating Kingfisher

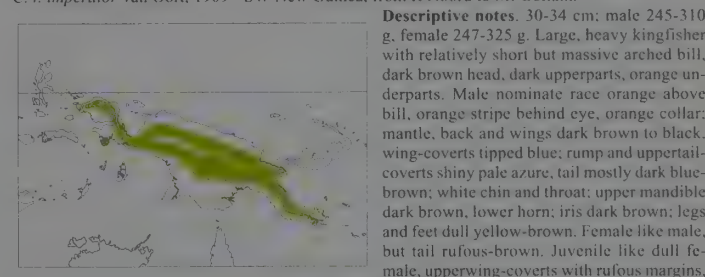
**Taxonomy.** *Clytoceyx rex* Sharpe, 1880, East Cape, New Guinea.

Possibly related to *Dacelo* and *Melidora*. N population described as race *septentrionalis*, but plumage variation is not constant. Two subspecies recognized.

**Subspecies and Distribution.**

*C. r. rex* Sharpe, 1880 - W, C & SE New Guinea, from Vogelkop I to Finisterre and Owen Stanley Range.

*C. r. imperator* van Oort, 1909 - SW New Guinea, from R Noord to Mt Goliath.



**Descriptive notes.** 30-34 cm; male 245-310 g, female 247-325 g. Large, heavy kingfisher with relatively short but massive arched bill, dark brown head, dark upperparts, orange underparts. Male nominate race orange above bill, orange stripe behind eye, orange collar; mantle, back and wings dark brown to black, wing-coverts tipped blue; rump and upper tail-coverts shiny pale azure, tail mostly dark blue-brown; white chin and throat; upper mandible dark brown, lower horn; iris dark brown; legs and feet dull yellow-brown. Female like male, but tail rufous-brown. Juvenile like dull female, upperwing-coverts with rufous margins,

neck and breast feathers with dusky brown margins. Race *imperator* larger. **VOICE.** Call of 3-4 clear liquid notes lasting 1 second, descending, final note slightly separated, given shortly after dawn from crown of tall tree, tail flicking with each note; also series of 8-10 monotonous upward-inflected whistles at 1-second intervals, "wu, wu, wu, wu, wu..."; alarm a guttural chatter; responds to playback of taped calls by flying overhead and calling "kik-kik-kik... kik-kik... kik-kik".

**Habitat.** Lowland and hill rainforest to 2400 m, but found mainly on hills and lower mountains in wet forest, forest edges, garden borders, and thickly wooded valleys and wet ravines. Recorded in mossy forest on Mt Kaindi, also in *Araucaria* plantations. Often perches in forest understorey, 6 m from ground.

**Food and Feeding.** Earthworms (Oligochaeta), insects and their larvae, snails (Gastropoda), lizards and snakes; said also to take small mice; an early report of feeding on crabs requires confirmation. Forages on ground, often around buttress roots of forest trees; ploughs up a patch c. 20 x 30 cm to depth of 8 cm by thrusting its bill into the ground at a slight angle and then pushing forward, occasionally moving the head from side to side; jerks head up, snapping bill and flicking off attached mud, pauses for a few seconds in erect and alert stance before resuming shovelling. A large earthworm was observed being pulled sideways from the ground. Captured birds frequently have damp earth caking the inside and outside of the bill. Probably forages at night, perhaps even more so than by day.

**Breeding.** Male collected in Jan had enlarged testes, and 2 in Jan had noticeable brood patches. A fledgling purchased in Oct from a market near Wau was said to be one of 2 taken from a tree-hole nest. No other information on any aspects of breeding.

**Movements.** Presumed to be sedentary.

**Status and Conservation.** Not globally threatened. Widely distributed in New Guinea in suitable habitat, but apparently uncommon. Information required on its breeding biology, as well as on its population level.

**Bibliography.** Andrew (1992), Beehler (1978), Beehler, Burg *et al.* (1994), Beehler, Pratt & Zimmerman (1986), Bell (1981), Coates (1985), Diamond (1972), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Gilliard & LeCroy

(1961), Gregory (1995c), Gyldenstolpe (1955b), Iredale (1956), Knowles & Nitchen (1995), Mayr & Rand (1937), Paludan (1935), Rand (1938, 1942a, 1942b), Rand & Gilliard (1967), Ripley (1964), Safford & Smart (1995), Tomlinson (2000), Weston (1975).

## Genus *LACEDO* Reichenbach, 1851

### 18. Banded Kingfisher

#### *Lacedo pulchella*

**French:** Martin-chasseur mignon    **German:** Wellenliet    **Spanish:** Martin Cazador Chico

**Taxonomy.** *Dacelo pulchella* Horsfield, 1821, Java.

Possibly an early offshoot of *Dacelo* lineage, with some resemblance to *Tanyptera*. Form from N Malay Peninsula, described as race *deignani*, is an intergrade between *amabilis* and *pulchella*. Three subspecies recognized.

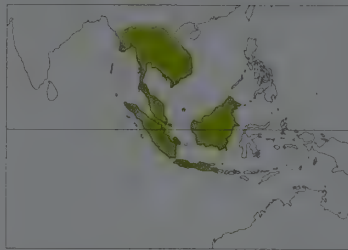
#### **Subspecies and Distribution.**

*L. p. amabilis* (Hume, 1873) - S & SE Myanmar E to C Vietnam (C Annam) and S to S Thailand and S Indochina.

*L. p. pulchella* (Horsfield, 1821) - S Thailand S to N Natuna Is and Sumatra (including Riau Archipelago), and E to Java.

*L. p. melanops* (Bonaparte, 1850) - Bangka I (off SE Sumatra) and Borneo.

**Descriptive notes.** 20 cm. A small kingfisher, barred above, which regularly raises and lowers crown feathers. Male of nominate race has bright blue crown with some black and white banding and speckling, rufous forehead, cheeks and collar; upperparts, wings and tail barred black and blue; chin, throat and centre of belly white, rest of underparts pale orange; bill red; iris yellow-brown; legs and feet pale pinkish-brown. Female very different, entire head and upperparts banded rufous and black, underparts white or buffy with narrow barring on breast and flanks. Juvenile duller than adults, more barring below, upper mandible brown, lower mandible orange with pale tip. Race *melanops* black cheeks and collar in male; *amabilis* slightly larger, male hindneck same colour as crown, female deeper rufous. **VOICE.** Long whistle, "wheeeoo", followed by 15 short,



trisyllabic "chiuiu" or "taweo" whistled notes at constant speed, becoming softer after 1 or 2 initial loud notes, disyllabic later in series; also sharp "wiak", singly or repeated.

**Habitat.** Lowland rainforest and bamboo-forest, hill forest, also secondary growth, peatswamp-forest and submontane forest; to 1100 m. In Borneo occurs to 1700 m in forest of headwater streams, and on Mt Kinabalu more common above 800 m than in the lowland forest.

**Food and Feeding.** Variety of insects, including grasshoppers and locusts (Orthoptera), katydids (Tettigoniidae), crickets (Grylloidea), cockroaches (Blattidae), cicadas (Cicadidae),

stick-insects (Phasmida), beetles (Coleoptera) and larvae, also millipedes (Diplopoda), centipedes (Chilopoda), woodlice (Oniscoidea); occasionally small fish and lizards. Hunts from high and low perches, typically perching motionless for lengthy periods; also hawks for insects among foliage in subcanopy level and in forest corridors, and comes down to fallen trees and forest floor. May probe in the ground.

**Breeding.** Lays in Jan-May. Nest excavated in rotting tree trunk, or in bank, or in nest of arboreal termites (*Eutermes*), up to 3 m above ground. Clutch 2-5 eggs. No information on incubation and fledging periods.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Widespread, and generally uncommon to fairly common; more frequent in Malay Peninsula. Extinct in Singapore for at least 40 years. Occurs in Khao Yai National Park and Khao Nor Chuchi (Khao Pra Bang Khram Non-Hunting Area), Thailand; in Nam Bai Cat Tien National Park and Bach Ma National Park, Vietnam; in Panti Forest Reserve and Taman Negara National Park, Peninsular Malaysia; and in Way Kambas National Park, Sumatra, and Baluran National Park, Java. Forest clearance in much of range likely to pose a threat.

**Bibliography.** Andrew (1992), Baker (1934a, 1934b), van Balen (1999), Bangs & Van Tyne (1931), Chasen & Hoogerwerf (1941), Deignan (1945), Delacour & Jabouille (1940), Duckworth (1996), Duckworth & Kelsh (1988), Duckworth, Salter & Khounboline (1999), Duckworth, Wilkinson *et al.* (1997), Gore (1968), Hellebrekers & Hoogerwerf (1967), Hoogerwerf (1949c, 1970), Jeyarajasingam & Pearson (1999), Lekagul & Round (1991), MacKinnon (1988), MacKinnon & Phillipps (1993), van Marle & Voous (1988), Medway & Wells (1976), Mees (1986), Riley (1938), Robson (2000a), Robson *et al.* (1993b), Smythies (1986, 1999), Verheugt *et al.* (1993), Wells (1985, 1999), Wildash (1968), Wiles (1979), Wilkinson, Dutson & Sheldon (1991).







19

ssp tyro

ssp archboldi

20

♀

ssp leachii

♂

ssp intermedia

♂

21

ssp cervina

♀

ssp occidentalis

♂

22

PLATE 11

inches 4  
cm 10



## Genus *DACELO* Leach, 1815

### 19. Rufous-bellied Kookaburra

#### *Dacelo gaudichaud*

**French:** Martin-chasseur de Gaudichaud **German:** Rotbauchliest **Spanish:** Cucaburra Ventrirrufa  
**Other common names:** Gaudichaud's Kookaburra, Rufous-bellied Giant Kookaburra

**Taxonomy.** *Dacelo gaudichaud* Quoy and Gaimard, 1824, Waigeo. Possibly the ancestral form of the genus *Dacelo*. Has in past been placed with *D. tyro* in genus *Sauromarptis*. Monotypic.

**Distribution.** Lowlands of New Guinea, along with W Papuan Is (Gebe, Waigeo, Batanta, Salawati, Misool, Kolepom), all islands in Geelvink Bay, Aru Is, and Heath Is (Sariba) in Milne Bay.

**Descriptive notes.** 28-31 cm; male 110-161 g, female 138-170 g. Large, distinctively marked kingfisher. Male has white stripe behind eye, glossy black cap and back separated by complete white collar; lower back, rump and uppertail-coverts shiny azure-blue; wing-coverts black, edged with pale blue; tail dark blue; underparts below throat rich cinnamon-rufous; bill whitish or yellowish-horn, often with dark line on culmen; iris dark brown; legs and feet greyish. Female like male, but tail rich chestnut. Juvenile dusky edges to feathers on hindneck and underparts, dusky bill. **VOICE.** Common calls are a loud, repeated "tok" or "chok", a very rapid "tok-tok-tok" sounding like "trrrk", repeated every 2 seconds, a series of loud hoarse barks or laughs at one pitch and either slow or fast, i.e. 1 or 2 per second; these calls often stimulate birds in adjacent territories to respond; several birds calling together can sound like chorus of *D. leachii*; also loud rattle in flight, which as bird alights can become a laugh, "kikikikiki-haw-haw-haw-haw-haw"; other calls include 3-6 slow, high-pitched shrieks as "clew, clew, clew", rasping call when pursuing another in flight; weak whistle by immatures.

**Habitat.** Mainly in lower canopy of monsoon and riverine forest, but also in primary rainforest, floodplain-forest, parkland, secondary growth, thick coastal palm scrub, mangroves and gardens; also uses isolated patches of trees in cleared lands, and teak (*Tectona grandis*) or rain tree (*Samanea saman*) plantations. Requires presence of arboreal termitaria for breeding. Generally below 500 m, but recorded at up to 1300 m in NE (Mt Bosavi).

**Food and Feeding.** Arthropods, including grasshoppers and locusts (Orthoptera), stick-insects (Phasmida), beetles (Coleoptera), larvae, earthworms (Oligochaeta), and large spiders (Aranea); also crabs (Decapoda); also small vertebrates, such as frogs, lizards, birds and small mammals. Forages mainly in lower canopy, taking prey from tree limbs and among the foliage; occasionally observed on ground, where sometimes digs. Attacks birds caught in mist-nets; is mobbed by small birds, suggesting that it may rob nests.

**Breeding.** Most breeding activity in late dry and early wet seasons; nest excavation reported in mid-Aug and Sept, but also in May-Jun; eggs reported in early Oct, and nestlings in Oct, Dec, Jan and early Feb. Both adults excavate tunnel with nest-chamber in an active termite nest, generally high up (2-40 m) on side of a forest tree. Territory 2-2.5 ha, defended by male, chasing away conspecifics and some other species. Clutch 2 eggs; no data on incubation and nestling periods; young fed by both parents, on mainly small insects but some large ones, also earthworms, 6-11 feeding visits per hour.

**Movements.** Sedentary.

**Status and Conservation.** Not globally threatened. Widely distributed in New Guinea, and common in suitable habitat. Occurs in Wasur National Park, Irian Jaya. Density of 1 bird/ha recorded. No information on any possible threats.

**Bibliography.** Andrew (1992), Bailey (1992), Beehler (1978), Beehler *et al.* (1986), Bell (1970c, 1975b, 1982a), Coates (1985), Diamond (1972), Diamond & Terborgh (1968), Finch (1980b), Fletcher (2000b), Gilliard & LeCroy (1968), Greenway (1966), Gregory (1995a, 1995c), Hiaso *et al.* (1994), Hindwood (1959), Hoogerwerf (1971), Mackay (1980), Mayr & Rand (1937), Mees (1965, 1982), Pearson (1975b), Rand (1942a, 1942b), Rand & Gilliard (1967), Ripley (1964), Safford & Smart (1995), Schodde & Hitchcock (1968), Weston (1975).

### 20. Spangled Kookaburra

#### *Dacelo tyro*

**French:** Martin-chasseur pailleté **German:** Aruliest **Spanish:** Cucaburra Escamosa  
**Other common names:** Aru Giant/Mantled Kingfisher, Aru Kookaburra

**Taxonomy.** *Dacelo tyro* G. R. Gray, 1858, Aru Islands.

Has been placed in *Melidora*, but seems much closer to other *Dacelo*. In past was sometimes placed in monotypic genus *Capricia*, or in *Sauromarptis* along with *D. gaudichaud*; possibly derived from an ancestor of latter on Aru Is which subsequently reinvaded adjacent mainland. Two subspecies recognized.

**Subspecies and Distribution.**

*D. t. tyro* G. R. Gray, 1858 - Aru Is.

*D. t. archboldi* (Rand, 1938) - S New Guinea, from R Bian and Habé I to R Wassi Kussa and Dimississi.

**Descriptive notes.** 33 cm; male 128-145 g, female 148-165 g. Male nominate race head, hindneck and mantle yellow-buff with black margins to feathers, back and scapulars black, rump and uppertail-coverts bright cobalt-blue; tail and wings blue-black, lesser and median wing-coverts edged with bright blue; chin and throat white, rest of underparts washed buff to pale orange; upper mandible black, lower mandible pale horn; iris dark brown; legs and feet grey to yellowish-grey. Distinguished from *D. leachii* by smaller size, darker head and back, dark eye. Female like male, but blue markings duller and with greenish tinge. Juvenile head dusker, underparts with narrow black margins. Race *archboldi* paler blue wing-coverts, paler underparts. **VOICE.** Series of loud, throaty "kurk" notes, similar to those of *D. leachii*, and has been reported calling in unison with that species.



air and amongst the foliage.

**Breeding.** Females in breeding condition and about to lay collected in Mar; nests with young found in Mar. Nest excavated in hemispherical termitarium; 2 nests were 5 m above ground, in termitaria 45 cm and 60 cm in diameter, one on *Alstonia scholaris* and other on *Acacia mangium*; unconfirmed reports of nesting in tree-holes. No information on clutch size, or on incubation and fledging periods.

**Movements.** Presumed to be sedentary.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in Trans-Fly EBA. Reported to be common in suitable habitat on the mainland; occurs in Wasur National Park, Irian Jaya. No recent reports from Aru Is. Limited distribution in S New Guinea could lead to problems for this species in the future.

**Bibliography.** Andrew (1992), Beehler *et al.* (1986), Bell (1981), Bellchambers *et al.* (1994), Coates (1985), Finch (1980b), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Hoogerwerf (1964), Knowles & Nitehen (1995), Mees (1982), Rand (1938), Rand & Gilliard (1967), Stattersfield *et al.* (1998), Stronach (1989), Weston (1975).

### 21. Blue-winged Kookaburra

#### *Dacelo leachii*

**French:** Martin-chasseur à ailes bleues **German:** Haubenliet **Spanish:** Cucaburra Aliazul  
**Other common names:** Northern Blue-winged Kookaburra, Fawn-breasted/Leach's Kingfisher, Barking/Howling Jackass

**Taxonomy.** *Dacelo leachii* Vigors and Horsfield, 1827, Keppel Bay, eastern Australia.

Racial differentiation difficult to assess, as distribution is almost continuous, and plumage colours affected by environmental factors (darker in wetter areas); variously treated as comprising from one to up to five races in Australia; proposed race *mungi*, formerly united with *occidentalis*, now included within nominate; *cliffoni* is synonym of *occidentalis*; *superflua* from S New Guinea and *kempi* from N Queensland (Cape York Peninsula) are insufficiently distinct to be accepted. Four subspecies currently recognized.

**Subspecies and Distribution.**

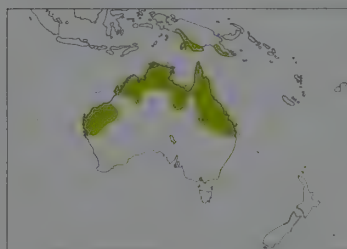
*D. l. intermedia* Salvadori, 1876 - S & SE New Guinea, from R Mimika to R Fly and from R Eloa to Amazon Bay.

*D. l. cervina* Gould, 1838 - Melville I, off Northern Territory.

*D. l. leachii* Vigors & Horsfield, 1827 - across N Australia E to Cape York Peninsula, S to Broome in W and to Brisbane (rarely, to Byron Bay) in E.

*D. l. occidentalis* Gould, 1870 - Hamersley and Pilbara Regions of Western Australia.

**Descriptive notes.** 38-41 cm; male 250-322 g, female 260-370 g. Very large, distinctive kingfisher, with pale head and eye, blue wings and rump. Male nominate race faintly dark-streaked head, grey-brown mantle and scapulars, blue tail with blue-barred white outer feathers; white underparts faintly vermiculated grey; upper mandible brownish-black, lower mandible creamy horn to pale yellow with dark basal triangle; iris white or very pale yellow; legs and feet pale flesh-brown to greenish-grey. Female slightly larger than male, rufous tail and uppertail-coverts, tail barred with blue-black. Juvenile like female, but crown paler, breast



feathers edged with dusky brown. Race *intermedia* larger and darker above, with head strongly streaked, blackish back, plain white below, upper mandible blackish; *cervina* smaller, darker above and below, breast buffy; *occidentalis* has whiter head, buff-washed underparts. **VOICE.** Loud chorus by 2 or more birds, particularly at dawn or dusk, up to 8 groups calling in turn, typically consists of introduction with repeated "Bark Calls", first duet with male and female giving series of independent and partly overlapping calls, then interchange with yelps and cackles, second duet again independent elements, often with hoarse "Screech Call", and abrupt finish with terminal "Cackle" or may extend into third duet. Other simple calls may also form elements of chorus: short, sharp "kuck" maintains contact in group, "Short Laugh" as "aa-aah-oo-oo" indicates location of bird, "Cackle" of 6 sharp elements, descending in pitch, precisely locates caller, "Grumble" a soft squawk indicating intention to fly, soft high-pitched "Piping" indicates intention to feed young, "Squawk" of 1-3 hoarse notes associated with courtship feeding, feeding young and young begging, "Chuckle" as soft rolling "o-o-o-o" associated with copulation, raucous "Screech Call" when attacked by predator or handled by person; short, harsh, high-pitched "aah" alarm when raptor flies over or other predator nearby. Calls of young change from soft squeaks to deeper squawks, which can be given incessantly.

**Habitat.** Savanna woodland and eucalypt (*Eucalyptus*) open woodland and forest, tall trees and woodland along watercourses, riverine and littoral mangrove and monsoon forest; avoids areas with dense understorey. Also in pasture and cultivated land with stands of trees, plantations far from water, and large suburban parks and gardens. Mainly in lowlands in New Guinea, but locally to 600 m. Where overlaps with *D. novaeguineae*, is usually more common away from water.

**Food and Feeding.** Wide variety of animals, mainly invertebrates, grasshoppers (Acrididae, Tettigoniidae), crickets (Gryllacridae, Gryllidae), mantids (Mantodea), stick-insects (Phasmida), beetles (Buprestidae, Carabidae, Cerambycidae, Curculionidae, Dytiscidae, Elateridae,



Scarabaeidae), bugs (Belostomatidae, Cydinidae, Reduviidae), cicadas (Cicadidae), ants (Formicidae), bees (Megachilidae), wasps (Pompilidae, Scolioidea, Tiphidae), insect larvae, centipedes (Chilopoda), millipedes (Diplopoda), spiders, scorpions (Scorpiones), crabs, crayfish (Parastacidae), snails (Gastropoda), earthworms (Oligochaeta); also small vertebrates, including small fish, frogs, lizards (Agamidae, Pygopodidae, Scincidae, Varanidae), snakes (Colubridae), freshwater terrapins (Testudines), small birds (*Zosterops*) and injured birds up to size of small doves (e.g. *Geopelia*, *Geophaps*), also bird eggs, and small mammals. At Kakadu National Park (Northern Territory), direct observations of prey taken indicated 59% invertebrates, 41% vertebrates, and analysis of pellets from nest-sites indicated that invertebrates constituted 45% by weight (73% by number) and vertebrates 55% by weight (28% by number). Perches on branches, posts or wires, usually 2-4 m from ground, scanning for prey; dives down to take it, usually from ground, just before or on landing, then returns to perch, or remains on ground to beat prey before swallowing it. Small prey dealt with quickly, larger items, particularly snakes, get repeated bashing; reptiles swallowed head first; with larger prey, the tail may protrude from bird's bill for some time. May also fly out to take prey from tree trunks, twigs, leaves; rarely, snatches winged green ants from the air. Also, makes shallow dives into water, and digs in soft, wet ground for earthworms. Attends bush fires to catch fleeing animals, and will try to take birds caught in mist-nets.

**Breeding.** Lays in Sept-Jan. Monogamous. Breeds as pair or as group of up to 12, most often 3 individuals; group consists of breeding pair and auxiliaries, the offspring of previous years, 1-4 years old, which assist with territory defence, preparation of nest, incubation, and brooding and feeding nestlings and fledglings; in Kakadu National Park (Northern Territory), 66% of territories held groups, and 85% of auxiliaries were male. Mean territory size 0.4 km<sup>2</sup>, territory defended against conspecifics and *D. novaeguineae*; male courtship-feeding female, sometimes assisted by auxiliaries, and starts nest-showing, where male and female in turn fly to prospective nest-site, land, look inside; if a termitarium, tunnelling then begins, birds initially striking without landing, later landing and pecking at surface; copulation usually at roost, before or during chorus. Nest in unfilled tree hole, mainly of eucalypt (*Eucalyptus*), or excavated in ground termitarium of *Nasutitermes tridiae* or 4-30 m high in arboreal one of *N. graveolus*, or of other termite species in New Guinea; at Kakadu, mean height of nests in trees 9 m, in termitaria 1.5 m, average size of nest entrance 11 cm, mean height 13 cm, mean depth from entrance 67 cm. Clutch usually 2 or 3 eggs, records of up to 5 possibly result of more than one female laying, laying interval 2-3 days; rarely, re-lays if first clutch lost early in season; incubation by female continuously overnight, by both sexes and auxiliaries for 63-73% of time during day; incubation period, including non-continuous sitting before clutch complete, 25-26 days; hatching asynchronous, 1 day between first and second eggs, occurs early in morning; young hatch naked, pink and blind, pin-feathers emerge from wing at 7 days, eyes open at 14 days, maximum weight reached up to 10 days before fledging, may be 20% higher than fledging weight; largest chick will attack and even kill younger ones with hooked tip of upper mandible, which disappears around time of fledging; young brooded by female overnight, even when fully feathered, male and auxiliaries do more during day but spend only short time in nest after feeding in early stages; food passed directly to nestlings, seldom recovered if dropped; adults and young regurgitate pellets in nest, young attempt to defecate out through entrance but often too far away, so nest floor soon fouled; first young fledges after c. 36 days, second 1-4 (exceptionally 8) days later, third only if food plentiful; fledglings beg for many months, but most feeding stops after 2 months, serious foraging by young begins at 1-2 months, explore neighbouring territories at 3 months; juvenile females less likely to remain on natal territory. In Kakadu National Park, 85% of eggs hatched, 54-57% of eggs laid resulted in fledged young, and 22% of nesting attempts failed to produce any fledglings.

**Movements.** Generally sedentary, many adults remaining in same territory for at least 5 years. Local seasonal movements often involve shift to different habitat within territory, e.g. in N Australia from wet riverside vegetation to better-drained forest in summer wet season, or dispersal of young.

**Status and Conservation.** Not globally threatened. Fairly common over most of its range, becoming abundant in F Cape York Peninsula. Density of 0.05 birds/ha in woodland with a grass understorey in New Guinea. In N Australia, 0.1-0.2 birds/ha in Kakadu National Park and 0.08-0.72 birds/ha in Howards Peninsula; 0.03-0.14 birds/ha elsewhere in Australia. Suitable habitat destroyed by clearance of woodland and forest for farming, but in New Guinea this species is extending its range with forest clearance. Often hit by vehicles; 6 killed in 3-km stretch of road in N Australia, representing 13% of local population. Has bred successfully in captivity.

**Bibliography.** Andrew (1992), Barker & Vestejens (1989), Beehler *et al.* (1986), Bell (1967, 1970a, 1986), Bellehambers *et al.* (1994), Blakers *et al.* (1984), Coates (1985), Crawford (1972), Diamond & Terborgh (1968), Dow (1980), Dunn (1984), Eastman (1970), Frith & Hitchcock (1974), Gates (2000), Hall (1974), Higgins (1999), Hopkins (1957), Johnstone & Storr (1998), Keast *et al.* (1985), Lindsey (1992), Longmore (1978), Macdonald (1988), Mayr & Rand (1937), Mees (1982), Pizzey & Knight (1977), Rand (1942a), Rand & Gilliard (1967), Rutgers & Norris (1977), Schodde & Mason (1997), Schodde & Tidemann (1986), Serventy & Whittell (1976), Simpson & Day (1998), Storr (1973, 1980), Strahan (1994), Tolhurst (1993), Tomlinson (2000), Trounson & Trounson (1987), Weston (1975), Woinarski, Press & Russell-Smith (1989), Woinarski, Tidemann & Kerin (1988).

## 22. Laughing Kookaburra

### *Dacelo novaeguineae*

**French:** Martin-chasseur géant      **German:** Jägerliest      **Spanish:** Cucaburra Común  
**Other common names:** Kookaburra, Jackass, Brown/Giant/Laughing Kingfisher

**Taxonomy.** *Alcedo nova Guinea* Hermann, 1783, New South Wales.

Long known as *D. gigas*, but name *novaeguineae* (dating to same year) has priority; species does not occur in New Guinea, and Sonnerat's first description of it from there seems to have been a deliberate falsification. Two subspecies recognized.

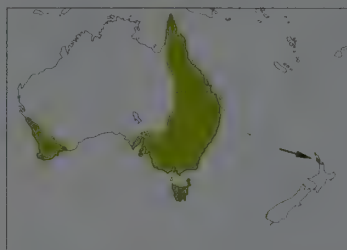
#### **Subspecies and Distribution.**

*D. n. minor* Robinson, 1900 - Cape York Peninsula, S to Cooktown.

*D. n. novaeguineae* (Hermann, 1783) - E Australia, from S Cape York Peninsula S to Flinders Range (South Australia) and Cape Otway (New South Wales).

Introduced (*novaeguineae*) to SW Australia, Kangaroo I, Flinders I, Tasmania and New Zealand (North I).

**Descriptive notes.** 39-42 cm; male 196-450 g (mean 307 g), female 190-465 g (mean 352 g). Very large, distinctive kingfisher. Male nominate race white head, dark crown and eyebrow, dark nape patch, dark brown upperparts, small blue rump patch, bluish-white tips of wing-coverts; rufous uppertail-coverts and tail banded with black; underparts white; upper mandible brownish-black, lower mandible horn-coloured with brown base; iris dark brown; legs and feet pale greenish to greyish-flesh. Differs from *D. leachii* in having much less blue on wings and rump, dark eye-mask, dark eye. Female larger, less blue on rump. Juvenile darker, more barred than adult. Race *minor* smaller, crown slightly darker. Voice. Well-known laughing choruses, mainly at dawn and dusk, by 2 or more birds, often in response to neighbouring group. Laugh has 5 elements: "Kooa", "Cackle",



"Rolling" as rapid repeated "ooo-ooo-ooo" for 2 seconds, "Haha" loudest element and lasting 2-5 seconds, and male's "Gogo" as loud distinct "go-go-go" or female's "Gurgle" as lower-pitched call with longer pauses; much individual variation in sequence of elements, some can be omitted, or rolling and haha elements repeated several times. Given singly, kooa call warns of birds of prey when deep and guttural, gets attention of others in group when softer; repeated "haha" used before attack; "Chuckle" equivalent to rolling element of laugh, repeated "ooo" sounds as contact; "Chuck Call" an abbreviated chuckle, when

feeding young; low-pitched "Squawk" a submissive call, by adults when begging for food; "Soft Squawk" when nest-showing; deafening "Screech Call" when two birds fighting. Violent head-shaking after preening sounds like a rattle. Nestlings quiet high-pitched squeak for first week, by 2 weeks incessant lower-pitched whirring call that becomes squealing squawk when adults arrive, used also in alarm; fledglings beg with soft persistent squawk, rising in intensity when adults approach, attempt first laugh at 6 weeks and competent by 3 months.

**Habitat.** Eucalypt (*Eucalyptus*) forest and woodland, using riparian trees along major watercourses to extend inland or into primary forest; also uses wooded and cleared farmland, city parks and suburban gardens, provided that tree hollows available for nesting; sometimes in forest edges, wetlands, pine plantations and forest regrowth. Where sympatric with *D. leachii* on Magnetic I (E Queensland), the species are interspecifically territorial; in other areas, *D. leachii* keeps to drier habitats.

**Food and Feeding.** Diet varied and well studied. Invertebrates recorded are earthworms (Lumbricidae, Megascolecidae), snails (Helicidae), spiders (Actinopodidae, Heteropodidae, Lycosidae), crabs, crayfish (Parastacidae), millipedes (Diplopoda), centipedes (Chilopoda), cockroaches (Blattellidae, Blattidae), beetles (Buprestidae, Carabidae, Cerambycidae, Chrysomelidae, Cleridae, Curculionidae, Dytiscidae, Elateridae, Geotrupidae, Latridiidae, Lucanidae, Passalidae, Scarabaeidae, Tenebrionidae), earwigs (Dermaptera), cicadas (Cicadidae), bugs (Lygaeidae, Nepidae, Pentatomidae), ants (Formicidae), moths (Hepialidae, Noctuidae), mantises (Mantidae), damselflies (Zygoptera), grasshoppers (Acrididae, Eumastacidae, Tettigoniidae), crickets (Gryllidae, Gryllotalpidae). Vertebrates include fish (Centropomidae, Cyprinidae, Embassidae, Pomatomidae, Percidae, Salmonidae), frogs (Myobatrachidae), lizards (Agamidae, Scincidae), snakes (Elapidae); seldom takes adult birds (Coturnix, Turnix, Phylidonyris), occasionally nestlings or fledglings (*Gallus*, *Anas*, *Cereopsis*, *Malurus*, *Manorina*, *Phylidonyris*, *Petroica*, *Pachycephala*, *Grallina*, *Corycolaptes*, *Arimimus*, *Carduelis*, *Passer*, *Sturnus*); some small mammals (*Cercartetus*, *Antechinus*, *Oryzotagus*, *Mus*, *Rattus*). In Tasmania, 26% beetles, 15% moths, 37% grasshoppers and crickets, 3% lizards; in New South Wales, 7% spiders, 14% beetles, 15% ants, 8% moths, 32% grasshoppers and crickets; items brought to a nest near Melbourne included 35% lizards and snakes, 32% insects, 15% earthworms, 8% crayfish, 1% rodents, and 7% birdtail scraps (cheese, raw meat, etc.). Most prey taken from ground, occasionally in flight or from shallow water; insects sometimes taken in flight or from tree trunks, but mainly from ground; aquatic prey taken by surface-plunging. Spends long periods watching from a branch or powerline, 1-10 m above ground; when prey seen, swoops down, wings folded or partly folded, spreading them just before landing beside prey and immediately seizing it in bill. Occasionally digs in ground for prey. Small items swallowed whole; larger animals sometimes beaten against ground but more usually carried in bill back to perch, where beaten on branch before being swallowed; prey may also be moved back and forth in the bill to pulverize it. Snakes up to 1 m long are grabbed behind the head, beaten violently on ground or on a perch, then swallowed head first; sometimes snakes are dropped from a height to stun them. In some areas frequents refuse tips to take food waste, and often takes scraps at picnic areas and feeding tables. Sometimes steals prey from hawks (Accipitridae) or snakes. Undigested food regurgitated as pellets, which may accumulate under roosting places.

**Breeding.** Lays in Sept-Dec; occasionally 2 broods. Monogamous; pairs for life, maintains territory all year. Pair often accompanied by up to 4 or 5 of its offspring, most of which are males, which live as group in territory and jointly defend it; group-members keep in sight and sound of each other but feed separately, at night roost together in dense foliage; aggression within group usually between breeding pair and auxiliary, increases just before egg-laying; calling, particularly duets, increases 2-3 months prior to breeding, male courtship-feeds female from 6 weeks before laying and for a few days after; pair spends much time visiting old and new nest-sites, scratching at site or sitting in cavity. Territory advertised with dawn and dusk choruses and some boundary display-flights; most aggression between neighbours ritualized, but fights can occur leading to fatal injuries. Nest usually in natural hollow in dead or living tree, or excavated in arboreal termitarium (often of *Nasutitermes walkeri*) or in tree with rotten centre; occasionally digs hole in bank or cliff, masonry or haystack, or uses old stick nest or epiphytic staghorn ferns (*Polypodium*); 60% of nests in hole in living eucalypt (30 species recorded), 16% in arboreal termitarium, 8% in hollow in non-eucalypt tree, 7% in dead tree or stump, and 9% in other sites including nestboxes; nest-hole 20 cm to 60 m above ground, average 8 m, entrance usually 12-15 cm (8-40 cm) wide, nest-chamber 20-150 cm wide and 20-40 cm high; same nest may be used for many years, some for 5 consecutive years, once intermittently for 60 years. Clutch 1-5 eggs, usually 2-3, 5-egg clutches likely laid by more than one female, laid in morning or afternoon, interval of 24-48 hours between first and second, 17-96 hours between subsequent eggs; will re-nest if first clutch lost; incubation may start from first egg but often sporadic until clutch complete, period 24-29 days, helpers incubate for 5-32% of time; eggs hatch over several days, hatching naked, pink and blind, pin-feathers visible under skin at 4 days and emerge at 7-11 days, eyes open after 10 days, feathers on body break out of sheaths after 17-22 days, head feathers, remiges and rectrices after 22-27 days; all group-members feed, brood and defend chicks; brooding bouts lasted 21-92 minutes, 36% by male, 32% by female, 16% by auxiliaries, nest unattended 16% of time; auxiliaries provide 10-61% of food brought to nest; in Canberra (Australian Capital Territory) study, groups did not bring more food than single pairs; feeding rate increased until chick 18 days old, then decreased; adults do not remove faeces, older chicks try to defecate through entrance but often miss, thus fouling nest floor, which becomes infested with maggots; fledging after 32-40 days, brood taking several days to leave nest, pair and helpers feed them for at least 6-10 weeks further; immature females disperse at 1-2 years, males at 2-4 years. In Victoria, 65% of eggs hatched, 82% of hatchlings fledged, 81% of fledglings survived to independence; in Canberra, 90% of eggs hatched and 67% of nestlings fledged, 43% of last-hatched chicks and 10% of second-hatched chicks killed by older siblings. Nests raided by other birds, mammals, snakes and goannas (*Varanus*). Sexual maturity at 1 year, but most delay breeding for several years. Longevity in the wild up to 11-15 years.

**Movements.** Sedentary, with occasional temporary movements to exploit abundant prey; prior to breeding, auxiliaries may disperse into vacant breeding sites; 90% of ringing recoveries less than 10 km from ringing site. Some records from New Zealand possibly of birds blown across Tasman Sea during storms.



**Status and Conservation.** Not globally threatened. Common over most of its range, and has benefited from human settlement. Density varies between 0.04 and 0.8 birds/ha, giving estimated total population of as many as c. 65,000,000 individuals. Apart from successful introductions to SW Australia, Kangaroo I, Flinders I, Tasmania and New Zealand, its distribution has not changed in historical times. No real threats, but density declines in areas where farmland is converted to residential blocks.

**Bibliography.** Aston & Aston (1988), Barker & Vestjens (1989), Batey (1910), Blakers *et al.* (1984), Bockheim (1998), Boles (1993), Brown (1949), Chambers (1989), Chisholm (1934), Correll & Vaden (1981), Cunningham (1870), Eastman (1970), Emmerson (1982), England (1944), Falla *et al.* (1981), Fitri & Ford (1998), Foster

(1962), Frauca (1969), Frith & Frith (1997), Green *et al.* (1988), Hall (1974), Hermes & Williams (1979), Higgins (1999), Hindwood (1947), Hooper & Hooper (1982), Immelmann (1960), Johnstone & Storr (1998), Kinsky (1970), Legge (1999), Lever (1987), Lindsey (1992), Loyn (1980), Lysaght (1956), Macdonald (1988), Mees (1977a), Moon (1992), Morton & Parry (1974), O'Grady (1961), Packe (1960), Parry (1968a, 1968b, 1972, 1973a, 1973b), Paton (1989), Pizzey & Knight (1997), Poiani (1991), Pyper (1996), Ralph & Ralph (1973), Reyer & Schmidl (1988), Rice (1980), Roberts, N.L. (1961), Roberts, P. (1993), Robertson (1985), Rose (1997), Schodde & Tidemann (1986), Simpson & Day (1998), Smith (1992), Storr (1984b), Strahan (1994), Templeton (1992), Tomlinson (2000), Trounson & Trounson (1987), Vallenga (1965), Watson (1992), Watts (1999), Weber (1971), Wood (1996), Woods (1976).





# Genus *CARIDONAX* Cabanis & Heine, 1860

## 23. White-rumped Kingfisher

### *Caridonax fulgidus*

**French:** Martin-chasseur étincelant **German:** Glitzerhies **Spanish:** Alción Culiblanco  
**Other common names:** Blue-and-white/Glittering Kingfisher

**Taxonomy.** *Halcyon fulgidus* Gould, 1857, Lombok.

Sometimes placed in genus *Halcyon*, and also shows some similarities to *Dacelo*, *Tanyisptera* and *Actenoides*; distinctive, however, with no close allies, and better treated in monotypic genus. Two subspecies recognized.

#### Subspecies and Distribution.

*C. f. fulgidus* (Gould, 1857) - Lombok and Sumbawa (Lesser Sundas).

*C. f. gracilirostris* (Rensch, 1928) - Flores and Besar (Lesser Sundas).



**Descriptive notes.** 30 cm. Unmistakable. Both sexes nominate race blackish head, blue-black upperparts, wings and tail, contrasting brilliant white rump and lower back; cheeks and underparts plain white; bill bright red; iris red or orange-red, orbital ring red; legs and feet red or orange-red. Juvenile buffy underparts, yellowish-orange bill. Race *gracilirostris* slightly longer wing and tail, narrower bill. **VOICE.** Rapid series of 8-14 harsh notes, "kuff-kuff-kuff..." at 1 per second, or series of 2-36 loud, insistent, puppy-like yaps, "wáuh, wáuh, wáuh...".

**Habitat.** Primary and tall secondary rainforest,

also monsoon forest and bamboo-forest, and degraded forest, isolated woodland, wooded cultivation, and village scrub with tall trees; sea-level to 1700 m. Most frequent in primary semi-evergreen forest.

**Food and Feeding.** Insects and insect larvae. Foraging behaviour undocumented.

**Breeding.** Lays in Mar and possibly Jan in Flores, possibly in Feb or Mar in Sumbawa. Territorial. Nest in burrow in an earth bank. Clutch of 2 eggs and a single nestling have been collected from nests.

**Movements.** Presumed to be sedentary.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in Northern Nusa Tenggara EBA. Widespread, and fairly common; on Sumbawa, uncommon generally but fairly common locally. It seems to be able to survive in degraded forest and woodland after the loss of its primary-forest habitat. More information on its biology and status is urgently required.

**Bibliography.** Andrew (1992), Butchart *et al.* (1993, 1996), Coates & Bishop (1997), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Inskipp *et al.* (1996), Jepson (1997), Johnstone *et al.* (1996), Knowles & Nitchen (1995), Laubmann (1928), McKean (1989), Rensch (1931), Schmutz (1977), Stattersfield *et al.* (1998), Tomlinson (2000), Verhoeve & Holmes (1999), White & Bruce (1986).

# Genus *PELARGOPSIS* Gloger, 1841

## 24. Stork-billed Kingfisher

### *Pelargopsis capensis*

**French:** Martin-chasseur guriat **German:** Storchschnabelliess **Spanish:** Alción Picocigüena  
**Other common names:** Brown-headed Stork-billed Kingfisher

**Taxonomy.** *Alcedo capensis* Linnaeus, 1766, Cape of Good Hope; error = Chandernagor, West Bengal.

Genus sometimes merged into *Halcyon*; in past, genus name given as *Ramphalcyon*, but *Pelargopsis* has priority. Forms a superspecies with *P. melanorhyncha*. Mainland races intergrade to some extent; races *smithi*, *nesoecca* and *isoptera* of doubtful validity. Somewhat confused nomenclature: nominate race previously believed to refer to populations of Java; under that arrangement, Indian mainland birds were placed in race *guriat*; birds of Borneo formerly separated as either race *innominata* or race *javana*, with latter name at one stage erroneously thought to refer not to Javan birds but to those of Borneo. Fifteen subspecies currently recognized.

#### Subspecies and Distribution.

*P. c. capensis* (Linn aeus, 1766) - Indian Subcontinent (except W and extreme N) S to Sri Lanka.

*P. c. osmastoni* (Stuart Baker, 1934) - Andaman Is.

*P. c. intermedia* Hume, 1874 - Nicobar Is.

*P. c. burmanica* Sharpe, 1870 - Myanmar, Thailand and Indochina S to about Isthmus of Kra in Malay Peninsula.

*P. c. malaccensis* Sharpe, 1870 - from Isthmus of Kra S to Riau and Lingga Archipelagos.

*P. c. cyanopteryx* (Oberholser, 1909) - Sumatra, Bangka, Belitung and Borneo.

*P. c. simalurensis* Richmond, 1903 - Simeulue I, off NW Sumatra.

*P. c. sodalis* Richmond, 1903 - Banyak Is, off NW Sumatra.

*P. c. nesoecca* (Oberholser, 1909) - Nias I and Batu Is, off W Sumatra.

*P. c. isoptera* (Oberholser, 1909) - Mentawai Is, off W Sumatra.

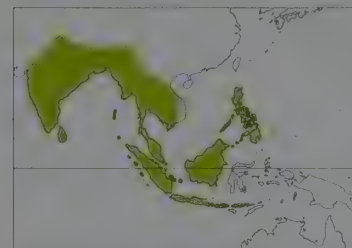
*P. c. javana* (Boddaert, 1783) - Java.

*P. c. floresiana* Sharpe, 1870 - Bali, Lombok, Sumbawa and Flores.

*P. c. gouldi* Sharpe, 1870 - N & W Philippines.

*P. c. smithi* (Mearns, 1909) - C & S Philippines.

*P. c. gigantea* Walden, 1874 - Sulu Archipelago (S Philippines).



**Descriptive notes.** 35 cm; male 143-180 g, female 182-225 g. Large kingfisher with huge bill. Both sexes nominate race olive-brown head, whitish chin, buff neck and underparts; upperparts dark green-blue, wings and tail bluer, rump azure; bill scarlet, darker at tip; iris dark brown; legs and feet orange-red. Juvenile dusky edges to feathers of breast and hindneck. Races vary in size, and in colour of back and wings and of head and underparts: *gigantea* large, head and underparts creamy white, paler blue-green above; *gouldi* richer rufous-buff; *burmanica* darker grey-brown cap, orange-buff below; *malaccensis* dark brown

cap well defined, upperparts dark blue. **VOICE.** A loud harsh "kak kak kak kak...", becoming softer; shrill descending whistle, "tree-trew" or "kwee-kwau"; very loud cackling "kie-iek, kie-iek, kie-iek"; pleasant song-like "peer...peer...purr"; loud sharp "wiak-wiak" when disturbed; in flight a screaming laugh, "kiu-kiu, kee-kiu", usually repeated several times.

**Habitat.** Generally found in lowland waterside habitats such as the forested edges of streams, canals, large rivers, reservoirs, lakes and seashores, at up to 800 m, but to 1200 m in India and Borneo. Occurs deep in primary rainforest, bamboo-forest and mangroves, but also in more open areas such as coconut plantations and paddyfields; often seen perched on mangrove roots on seashore. In Peninsular Malaysia frequent in mangroves in NE, but apparently not found in mangroves in NW, where *P. amauoptera* occurs.

**Food and Feeding.** Feeds mainly on marine and freshwater fish, crabs and other crustaceans, but also takes frogs, lizards, rodents, young birds, also insects (Coleoptera) and insect larvae. Perches quietly on still roots in mangroves or on branch overhanging water, typically 2-4 m above the water, watching for prey and occasionally bobbing head or wagging tail; sits vertically, with bill inclined at 40° below horizontal; plunges down at steep angle into water or on to land to capture prey, which is then taken back to the perch and banged against branch a few times to immobilize it, before being swallowed. Recorded following foraging smooth-coated otters (*Lutra perspicillata*) and taking prey items disturbed by them.

**Breeding.** Lays in Jan-Sept in India, in Jan-May and Aug-Sept in Sri Lanka, in Apr in Nicobar Is and Philippines, in Feb-Apr in Myanmar, in Mar and Apr in Malaysia, in May-Jun in Singapore, and in Jan-Feb in Java. Monogamous; territorial, aggressively maintains territory against conspecifics and against other birds up to size of White-bellied Sea-eagle (*Haliaeetus leucogaster*) and Lesser Adjutant (*Leptoptilos javanicus*). Nest excavated in a riverbank, or decayed tree trunk, or ground or arboreal terrarium, up to 10 m above ground; both sexes fly at the site and hit it with the bill, and, as wood or earth is loosened, they then perch and remove it with the bill; a pair repeatedly hit a brick wall, but made only a few small holes after several weeks; natural tree hollow also sometimes used; nest-tunnel 9-10 cm wide, up to 1 m long, ending in nest-chamber 23 cm in diameter and 13 cm high; a nest in a terrarium had tunnel 18 cm long and chamber 30 cm in diameter. Clutch 2-5 eggs; sometimes a second, or replacement, clutch may be laid in same nest; no information on incubation and fledging periods.

**Movements.** Sedentary, with some local movements; 5 birds ringed in S Thailand were recaptured at same place 14 months later, another moved 16 km to SE. Vagrant recorded in S China (S Yunnan).

**Status and Conservation.** Not globally threatened. Widespread and found in a variety of habitats. Locally common in some areas, but generally sparsely distributed; common in dry lowlands in Sri Lanka. Occurs in several protected areas throughout much of its range. Range may be diminishing, since there are apparently no recent records from Bali or Lombok.

**Bibliography.** Ali (1996), Ali & Ripley (1983), Baker (1934b), van Balen (1996), Bangs & Van Tyne (1931), Begbie (1906), Brown (1979), Bucknill & Chasen (1990), Burton (1978b), Chasen (1939), Coates & Bishop (1997), Daniels (1997), Danielsen *et al.* (1994), Deignan (1945), Delacour & Mayr (1946), Dickinson *et al.* (1991), Duckworth & Kelsh (1988), Duckworth *et al.* (1999), Edgar (1933), Fleming *et al.* (1976), Gore (1968), Grimmer *et al.* (1998), Harrison, C.J.O. (1961), Harrison, J. (1999), Harvey (1990), Henry (1998), Hoogerwerf (1949a, 1970), Inskipp, C. & Inskipp (1991), Inskipp, T. *et al.* (1996), Jayawardene (1989), Jayarajasingam & Pearson (1999), Junge (1936), Kennedy *et al.* (2000), Kruuk *et al.* (1993), Lamsfuss (1998), Lekagul & Round (1991), MacKinnon & Phillips (1993, 2000), Manuel (1941), van Marle & Voous (1988), McClure (1998), McGregor (1905), Medway & Wells (1976), Mees (1971, 1986), Meyer de Schauensee (1984), Oberholser (1909), Pfeffer (1958), duPont & Rabor (1973a, 1973b), Rabor (1938, 1977), Riley (1938), Ripley & Rabor (1958), Robson (2000a), Sharpe (1874), Smythies (1986, 1999), Stressemann (1952), Thompson (1966), Tikader (1984), Vowles & Vowles (1984), Wells (1999), White & Bruce (1986), Wyatt (1929), Zhao Zhengjie (1995).

## 25. Black-billed Kingfisher

### *Pelargopsis melanorhyncha*

**French:** Martin-chasseur à bec noir **German:** Schwarzschnabelliess **Spanish:** Alción Piquinegro  
**Other common names:** Dusky-faced/Great-billed Kingfisher, Celebes/Sunda Stork-billed Kingfisher

**Taxonomy.** *Alcedo melanorhyncha* Temminck, 1826, Sulawesi.

Genus sometimes merged into *Halcyon*; in past, genus name given as *Ramphalcyon*, but *Pelargopsis* has priority. Forms a superspecies with *P. capensis*. Three subspecies recognized.

#### Subspecies and Distribution.

*P. m. melanorhyncha* (Temminck, 1826) - Sulawesi and associated islands (Bangka, Manadotua, Lembeh, Togian Is, Dodepo, Wowoni, Kabaena, Muna, Butung, Labuandata, Salayar).

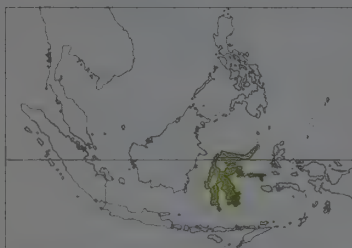
*P. m. dichrorhyncha* A. B. Meyer & Wigglesworth, 1896 - Banggai Is.

*P. m. eutreptorhyncha* Hartert, 1898 - Sula Is.

**Descriptive notes.** 35 cm; male 184 g, female 203 g. Large kingfisher characterized by pied plumage, large bill. Both sexes nominate race whitish head, dusky forehead and around eye, white mantle, rump and underparts, dark back, wings and tail, tail washed with blue; bill black, occasionally small dark red spot at base; iris dark brown; legs and feet dark red-brown. Juvenile dark brown fringes to feathers on hindneck and breast. Race *dichrorhyncha* larger, has deep red bill with black tip; *eutreptorhyncha* intermediate in size, less red at base of bill. **VOICE.** Loud, barking "kak-kak-kak", or repeated "ke-kak", also series of yapping sounds.

**Habitat.** Estuaries, mangroves, coastal scrub and wooded seashores, shrubby sea cliffs, coastal islets and coastal villages with trees; also found inland on large rivers, creeks in woodland and lightly wooded





National Park, Lore Lindu National Park and Tangkoko DuaSudara Nature Reserve. No recent records from S Sulawesi. More information on its biology is urgently needed.

**Bibliography.** Andrew (1992), Andrew & Holmes (1990), Baltzer (1990), van Bemmel & Voous (1951), Catterall (1997), Coates & Bishop (1997), Davidson *et al.* (1995), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Gregory-Smith (1998), Holmes & Philipps (1996), Indrawan, Masala & Pesik (1997), Inskipp *et al.* (1996), Jepson (1997), Knowles & Nitchen (1995), Rozendaal & Dekker (1989), Stones *et al.* (1997), Stresemann (1940), Wardill (1995), Wardill *et al.* (1999), Watling (1983), White & Bruce (1986).

## 26. Brown-winged Kingfisher

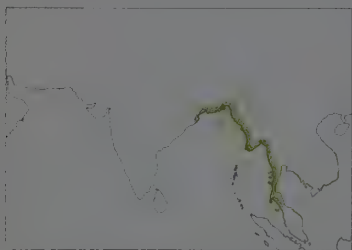
### *Pelargopsis amauroptera*

**French:** Martin-chasseur à ailes brunes **German:** Braunflügelst **Spanish:** Alción Alipardo  
**Other common names:** Brown-winged Stork-billed Kingfisher

**Taxonomy.** *Halcyon Amauropterus* Pearson, 1841, Calcutta, India.

Genus sometimes merged into *Halcyon*; in past, genus name given as *Ramphalcyon*, but *Pelargopsis* has priority. Species name sometimes given as *amauropterus*, but is Latinized Greek adjective and must agree with feminine genus name; claimed to be a noun in apposition, but no internal evidence for this. Monotypic.

**Distribution.** E India (from Orissa) E along coast and islands to Myanmar, then S, including Mergui Archipelago, to W coast of Thailand and to islands of NW Peninsular Malaysia.



**Descriptive notes.** 35 cm; male 162 g. Large coastal kingfisher with large red bill. Both sexes pale orange head and underparts, dark brown back, wings and tail, brilliant blue rump; bill scarlet with dusky tip; iris dark brown, orbital skin red; legs and feet scarlet with black nails. Distinguished from *P. capensis* by brown, not blue, back, wings and tail. Juvenile scalloped pattern on wing-coverts and breast, red bill with brownish tip. **VOICE.** Call a harsh, cackling, repeated "chak-chak-chak-chak", also short, descending sequence of whistles, "tree, treew-treew".

**Habitat.** Mainly coastal, in mangroves, tidal

forest, mudflats, estuaries and brackish creeks, and moves out on to quiet rocky shores; appears to prefer old-growth mangroves. Seldom seen beyond tidal limits, but may move a few km inland on larger rivers, and reported from wooded rim of a sinkhole lake.

**Food and Feeding.** Crabs and fish. Prey are detected from perches in mangroves; catches crabs by flying down low to land on the mud and rapidly seize one; dives into the water for fish; large prey are carried back to a perch in the bill, struck against the perch, and then repositioned before being swallowed. Seen to dive into surf for prey, settling on sand to secure the item while waves broke over it. Also exploits small crabs that swarm across mudflats at low tide.

**Breeding.** Lays in Mar-Apr in India. Nest in burrow dug into a mud bank or cliff by a creek, burrow 10 cm wide, 30-60 cm long, ending in chamber 20 cm in diameter; one nest-hole was 5 m high, just below top of bank. Clutch 3-4 eggs. No other information.

**Movements.** Presumably chiefly sedentary, but reported to be only non-breeding visitor in parts of W range; rarely, moves short distance inland from coast, and early record from NE Bangladesh at Sylhet, 250 km inland.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Widespread and locally common: rare in Orissa, but locally common in West Bengal and in Bangladesh; fairly common to locally common in SW Myanmar and Tenasserim; uncommon to locally fairly common in Thailand, and fairly common on NW Malaysian islands. No figures available on numbers, but total population possibly not very large. Continuing major clearance and degradation of mangroves in some areas is reducing its favoured habitat.

**Bibliography.** Ali & Ripley (1983), Baker (1934a, 1934b), Daniel & Hussain (1975), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Grimmett *et al.* (1998), Harvey (1990), Inskipp *et al.* (1996), Jeyarajasingam & Pearson (1999), Kazmierczak (2000), Knowles & Nitchen (1995), Lekagul & Round (1991), Majumdar *et al.* (1992), Medway & Wells (1976), Oberholser (1909), Pandav (1996), Riley (1938), Robson (2000a), Round (1988), Smythies (1986), Stattersfield & Capper (2000), Wells (1999).

cultivation, and swamps; when disturbed, flies off into forest. Sea-level to 600 m, locally to 980 m at Dumoga-Bone National Park.

**Food and Feeding.** Mainly crabs and crayfish. Perches on a branch above shallows and scans the water; plunges down for prey, which is brought back to perch and beaten before being swallowed.

**Breeding.** Birds in breeding condition in Sept on Muna and Butung. No other information.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Widely but sparsely distributed; common in some localities. Occurs in Dumoga-Bone

### Subspecies and Distribution.

*H. c. major* (Temminck & Schlegel, 1848) - NE China, Korea and Japan (Hokkaido S to Kyoto); migrates S to Philippines and Talaud Is.

*H. c. bangsi* (Oberholser, 1915) - Ryukyu Is, Taiwan and Lanyu I; migrates S to Philippines and Talaud Is.

*H. c. coromanda* (Latham, 1790) - Nepal E to N Myanmar and S China, S to W Bengal and S Thailand; N populations winter S to Malay Peninsula, Sumatra and Java.

*H. c. mizorhina* (Oberholser, 1915) - Andaman Is.

*H. c. minor* (Temminck & Schlegel, 1848) - S Thailand (from about Isthmus of Kra) S to Sumatra (including Simeulue I, Batu Is, Mentawai Is), Riau Archipelago, Bangka and Belitung, Java and Borneo.

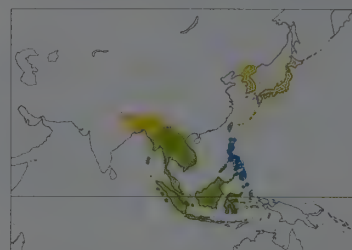
*H. c. lineae* Hubbard & duPont, 1974 - Palawan (SW Philippines).

*H. c. claudiae* Hubbard & duPont, 1974 - Tawitawi and Sanga Sanga (Sulu Archipelago).

*H. c. rufa* Wallace, 1863 - Talaud and Sangihe Is S to Sulawesi and offshore islands (Lembeh, Talisei, Togian, Muna, Butung).

*H. c. pelingensis* Neumann, 1939 - Banggai Is (Peleng, Banggai, Labobo).

*H. c. sulana* Mees, 1970 - Sula Is (Taliabu, Seho, Mangole, Sanana).



**Descriptive notes.** 25 cm; male 73-80 g, unsexed adults 60-92 g (Peninsular Malaysia). Medium-sized, rather distinctive, but shy kingfisher. Both sexes nominate race rufous-chestnut upperparts washed lilac, contrasting glossy azure-blue back and rump, paler rufous underparts; bill red or orange-red; iris dark brown, orbital skin red; legs and feet scarlet. Juvenile darker, duller, has dusky scallops on breast. Races vary in size, and in degree of violet or rufous coloration: *major* larger, paler than nominate, with less violet gloss, rump patch smaller; *minor* very small, much darker, washed with violet, large sil-

very rump patch; *lineae* even darker; *mizorhina* dark rufous with bright violet gloss, dark below with violet wash on breast. **VOICE.** Descending sequence of 4-5 loud, mournful whistles and a tremulous "quirr-r-r-r-r" in Malaysia; in India high-pitched shrill monosyllabic, in Japan repeated shrill metallic note or tremulous fluty "pyorr, pyorr" repeated at intervals; also 8-10 loud chattering notes for 3 seconds, sometimes louder and higher-pitched, also series of raucous disyllabic notes, the first syllable clear and piping upslur, second longer and downslurred, 1 note per second for up to 45 seconds (Sula Is.).

**Habitat.** In N temperate parts of range inhabits dense evergreen forest and temperate woodland around mountain streams at up to 1800 m, and cool, wet *Cryptomeria* groves; in S tropical parts more often near coast in mangroves, *Nipa* palms and tidal forest, also streams in forest, secondary growth, woodland and coconut plantations with shrubby understorey. In Malay Peninsula, residents found in mangrove forest and immediate landward fringe, but wintering migrants occur both in mangroves and farther inland, to 460 m. Remains in cover during day, but may emerge in evening to bathe.

**Food and Feeding.** Variable, depending on habitat: in terrestrial habitats insects, including beetles (Coleoptera), grasshoppers and locusts (Orthoptera), bugs (Homoptera), cicadas (Cicadidae), butterflies (Lepidoptera), bees (Apidae), also earthworms (Oligochaeta), land snails (Gastropoda), and lizards up to 8 cm long; in aquatic habitats, takes mayflies (Ephemeroptera), crabs and crayfish, frogs and tadpoles, newts and salamanders (Urodela), fish, and offal. Obtains prey by watching from a perch and then flying down on to ground or diving into water or surf, returning to perch with prey. Reports from Philippines of breaking open shells of land snails on stone anvils on forest floor need confirmation.

**Breeding.** Lays in Jun in S Korea, in Jun-Jul and possibly Aug in Japan; in Apr-May, possibly from Mar, in India; in May in S Peninsular Malaysia (Tioman I), in Feb/Mar and May in N Borneo, and in Feb-Mar in Sulawesi. Nest generally dug in a steep earth bank in India and Ryukyu, but tree hole up to 3 m above ground used in Japan, and other sites include arboreal termitarium, old hornet nest, thatched roof and village mud walls; male excavates mainly in morning; entrance 5 cm across, often concealed behind leafy vegetation, leads to tunnel 45-100 cm long ending in nest-chamber 15 cm wide and 12 cm high. Clutch 4-6 eggs; both sexes incubate during day, but only female at night; only female broods chicks; both sexes feed the young, in Japan mainly frogs (43-64%) but also fish (20-26%), lizards (10%) and invertebrates (5%).

**Movements.** Resident in S of range; some breeders in Malaysia remained at same site for at least 6 years. Migratory in N; migrating birds move at night, and are reported from forest and also offshore islands. Breeders present in NE China and Japan May-Sept, migrate through E China, Ryukyu Is and Taiwan to winter in Sulawesi from early Sept to Mar and in Philippines late Sept to mid-May; autumn movement through Taiwan not documented. Birds from Nepal and India E to Myanmar move through SE Asia, winter from S Thailand to Sumatra and Java; autumn migrants reported from Malay Peninsula Sept-Dec, return movement over Fraser's Hill in Apr and on Rok Is in early May. In Philippines and Malaysia wintering migrants returned to same site each year. A few individuals overwinter on breeding grounds in India and possibly Korea.

**Status and Conservation.** Not globally threatened. Very widespread, but generally considered rare or uncommon, although this possibly due to its shy, retiring habits. Occurs in several reserves, including Manas Wildlife Sanctuary in Bhutan, Cuc Phuong National Park in Vietnam, Tangkoko DuaSudara Nature Reserve and Dumoga-Bone National Park in Sulawesi, and Rajah Sikatuna National Park in Philippines. Clearance of mangroves, particularly of large trees needed for breeding, has almost certainly reduced its populations in the Thai-Malay Peninsula; residents seem to have disappeared from Singapore in 1980's; the longest interval between recaptures of an individual in Selangor mangroves was 71 months. In Java, recent records only from W. Some migrating birds are killed at lighthouses; in addition, over 40 stuffed specimens were recently seen for sale in a shop in Taiwan.

**Bibliography.** Ali (1996), Ali & Ripley (1983), Ali *et al.* (1996), Austin (1948), Austin & Kuroda (1953), Baker (1934a, 1934b), Brazil (1991), Coates & Bishop (1997), Danielsen *et al.* (1994), Davidson *et al.* (1995), Deignan (1945), Delacour & Mayr (1946), Dickinson *et al.* (1991), Duckworth *et al.* (1999), Erritzoe (1995), Etchécopar & Hùe (1978), Fleming *et al.* (1976), Gibson-Hill (1949b), Gore (1968), Gore & Pyong-Oh (1971), Grimmett *et al.* (1998), Hoogerwerf (1970), Hornskov (1996), Hubbard & duPont (1974), Inskipp & Inskipp (1991), Jeyarajasingam & Pearson (1999), Kennedy *et al.* (2000), Lekagul & Round (1991), Lim Kim Seng (1992), MacKinnon & Philipps (1993, 2000), van Marle & Voous (1988), McClure (1976, 1998), Medway & Wells (1976), Mees (1977b, 1986, 1991), Meyer de Schauensee (1984), Mima *et al.* (1988), Nakamura & Kashiwagi (1989), Nakamura *et al.* (1988), Oberholser (1915), duPont & Rabot (1973a), Rand (1954), Robson (2000a), Round (1988), Shimada (1984), Smythies (1986, 1999), Stepanyan (1990), Thompson *et al.* (1993), Tikader (1984), Wells (1999), White & Bruce (1986), Yamashina (1982), Zhang Cizu *et al.* (1997), Zhao Zhengjie (1995).

## Genus *HALCYON* Swainson, 1821

## 27. Ruddy Kingfisher

### *Halcyon coromanda*

**French:** Martin-chasseur violet **German:** Feuerliet **Spanish:** Alción Rojizo

**Taxonomy.** *Alcedo coromanda* Latham, 1790, Coromandel, India.

A distinctive species, not apparently very closely related to others in the genus; has been sometimes separated in monospecific genus *Entomothera*. Race *claudiae* included in *minor* by some authors. Ten subspecies recognized.



## 28. White-throated Kingfisher

*Halcyon smyrnensis*

**French:** Martin-chasseur de Smyrne      **German:** Braunliest      **Spanish:** Alción de Esmirna  
**Other common names:** White-breasted/Smyrna Kingfisher

**Taxonomy.** *Alcedo smyrnensis* Linnaeus, 1758, Izmir, west Turkey.

Forms a superspecies with *H. cyanoventris*, and sometimes considered conspecific, but recently found to overlap in range in W Java without interbreeding. Populations described as race *perpulchra* (Myanmar E to Indochina, S to Greater Sundas) and race *fokiensis* (S & E China, Taiwan) considered inseparable from *fusca*. Four subspecies currently recognized.

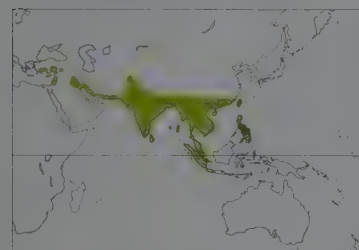
**Subspecies and Distribution.**

*H. s. smyrnensis* (Linnaeus, 1758) - W & S Turkey S to NE Egypt, and from C Iraq E to Pakistan, extreme NE Afghanistan and NW India.

*H. s. fusca* (Boddaert, 1783) - India (except NW) and Sri Lanka E to SE China and Taiwan, and S to Sumatra and W Java.

*H. s. saturator* Hume, 1874 - Andaman Is.

*H. s. gularis* (Kuhl, 1820) - Philippines.



**Descriptive notes.** 27-28 cm; male 85-88 g (*smyrnensis*), 76-87 g (*fusca*), 75-108 g (*gularis*), female 110 g (*smyrnensis*), 79-101 g (*gularis*). Medium-sized kingfisher with distinctive dark chestnut, blue and white plumage. Male of nominate race has dark chestnut head, flanks and belly, white throat and breast, blue back, wings and tail; lesser wing-coverts chestnut, median coverts dark blue; white patch at base of black primaries obvious in flight; bill red; iris dark brown, orbital skin red; legs and feet dusky red. Female slightly paler head and belly. Juvenile duller, breast with fine dark scallops. Race *fusca* smaller, slightly darker.

less green tinge in blues; *saturator* darker browns; *gularis* only chin and throat white. **Voice.** Song a loud trill or whistle reeling down scale over 2 seconds, followed by short downward-inflected trills, repeated regularly from high perch. "klililililililil hahahahaha, tirtt-r-o, tirtt-r-o, tirtt-r-o, tirtt-r-o"; loud cackle, "chake ake-ake ake-ake", often as contact-alarm as the bird flies; short "chik" while searching for prey, also trilling "ji-kurr", piercing "tsik", and prolonged "kit-kit-kit-kit" by female inviting copulation.

**Habitat.** Uses wide variety of habitats: dams, ponds, canals, creeks, swamps, mudflats, beaches with coconut palms and trees, mangrove edges, *Nipa* palm swamps, oil palm (*Elaeis guineensis*) plantations, farmland, rice fields, large gardens, roadside trees, light industrial sites, bamboo-forest, dry deciduous forest. Usually avoids dense forest except for clearings, but found in depths of teak forest in Myanmar. Less common above 2000 m, but occurs at up to 5000 m in Nepal. Territories include more open space than those of nearby *Todiramphus chloris*, and both are excluded from tree cover in Malay Peninsula by the larger *H. pileata*.

**Food and Feeding.** Wide variety of prey recorded. Insects include mole-crickets (*Gryllotalpa*), crickets and grasshoppers (Locustidae, Tettigidae, Gryllidae), earwigs (Labiduridae, Chelisochidae), cockroaches (Blattodea), bugs (Belostomatidae, Pyrrhocoridae) beetles (Dytiscidae, Dynastidae, Rutelidae, Meloidae, Cicindelidae), mantises (Mantodea), termites (Isoptera), winged ants (Formicidae), moths and caterpillars (Lepidoptera); also takes small scorpions (Scorpiones), centipedes (Chilopoda, including dangerous *Scelopendra*), snails (*Achatina*), crabs and crustaceans (Palaemonidae, Ocypodidae, Potamonidae, *Paratelpusa*), earthworms (Megascopidae), fish (Cyprinidae, Bagridae, Anabantidae), frogs and toads (*Rana*, *Bufo*), lizards (*Gecko*, *Draco*, *Calotes*, *Mabuya*), chameleons, snakes (*Coluber*, *Natrix*, *Ptyas* to 65 cm long), birds, voles, mice, and squirrels (*Funambulus*). In Bengal, fish (31%) composed most of the diet, followed by frogs and toads (19%), insects (16%), reptiles (14%) and crustaceans (11%), but fish component varied from 43% in wet season to 19% in dry season. Predation on fish fry in India most concentrated early in morning, 05:45-06:45 hours, and 79% of dives were successful. Birds both adults of small passerines (*Lonchura*, *Passer*, *Zosterops*) and nestlings (*Copsychus malabaricus*, *Passer montanus*, *Vanellus indicus*, *Lonchura*), and in Israel captures exhausted migrant Willow Warblers (*Phylloscopus trochilus*); also grabs birds from mist-nets. Typical sit-and-wait predator, spends long periods on perch 8-10 m above ground, with just head bobbing or tail wagging, before diving head first at 45° angle into deep water, or landing feet first in puddle or on ground; can hover for a moment over water before snatching prey. While still on ground or on returning to perch, will batter prey before swallowing it; can take up to 30 minutes before food swallowed. Termite alates caught on wing, and *Scarabaeus* beetles taken in flight over 1 hour after dusk; in Kashmir, feeding activity reported as largely crepuscular. Observed turning over earth in an arable field, seeking insects. Closely follows grazing cattle to catch insects disturbed by them.

**Breeding.** Lays in Jun in Egypt, in Apr-May in Israel and Iraq, mainly in Apr-Jul (Jan-Aug) in India, in Apr in Myanmar, mainly in Mar-Apr (Dec-Jun) in Sri Lanka, in Dec to early Aug in Malaysia, and in Mar-Apr in Thailand. Sumatra and Philippines: drop in water level may be external stimulus for laying; sometimes double-brooded. Monogamous, but presence of 3 birds in some areas suggests possibility of communal breeding. Calling from prominent perch, e.g. top of tree, increases at start of breeding season, bird sitting upright and periodically spreading wings to show white wing patches; in aerial display flies 50-60 m up with much calling, then spirals down. Nest usually in earthen bank of ditch, stream, river, pond or road cutting, sometimes in territarium, rock crevice, tree or mud hole, rarely in haystack; in Israel sometimes in nest-hole of bee-eater (*Merops*);

nest-chamber, up to 15-23 cm wide and 13 cm high, at end of inclined tunnel 30-150 cm long and 6-8 cm in diameter. Clutch 4-7 eggs, usually 5-6; both parents incubate, period 18-20 days; both also feed chicks, fledging period 26-27 days; adults feed young for 1 month after fledging.

**Movements.** Many populations, from Middle East across to S China (Hong Kong), exhibit partial short-distance migration, with seasonal changes in abundance, probably involving mostly juveniles. In Malay Peninsula resident in favoured habitat, with no retraps or recoveries more than 4 km from place of ringing; many ringed birds are recaptured frequently, but none more than 1 year later, possibly suggesting nomadism. Vagrants recorded in Greece, Cyprus, various Middle East countries including Syria, Saudi Arabia (Riyadh) and Kuwait, also former USSR, and individuals may move more than realized. In India and Pakistan often recorded in monsoon season at night at lights, in areas where normally absent.

**Status and Conservation.** Not globally threatened. Generally common throughout its range, and locally abundant. Nests 100 m apart at highest densities. Total numbers in Malaysia thought likely to have increased in latter decades of 20th century. Highly adaptable; ability to use farmland and low-lying oil palm plantations has allowed it to expand its range (e.g. in Sumatra, which it colonized in 1950's), possibly at the expense of *Todiramphus chloris*; conversely, seems to have been replaced by that species on Singapore. Has bred successfully in captivity.

**Bibliography.** Ali (1969, 1977, 1996), Ali & Ripley (1983), Arnold (1962), Asad-Akhtar & Tiwari (1993), Baker (1934b), Balasubramanian (1992), Bates & Lowther (1952), Beaman & Madge (1998), Beaman *et al.* (1975), van Bemmelen & van Lynden (1949), van den Berk & Kasparek (1988), Biscoe (1900), Burton (1998), Cramp (1985), Csorba *et al.* (1997), Danielsen *et al.* (1994), Deudhikari & Bhattacharyya (1982), Deignan (1945), Dementiev & Gladkov (1951), Dickson *et al.* (1991), Duckworth *et al.* (1999), Edgar (1933), Eshkol (1983), Étchécopar & Hue (1964, 1978), Evans, M.I. (1994), Fleming *et al.* (1976), Fry *et al.* (1988), Gibson-Hill (1948, 1949b, 1952a, 1952b), Grimmett *et al.* (1998), Harper (1900), Harrison (1999), Harvey (1990), Henry (1998), Holmlom *et al.* (1988), Holmes (1996), Hoogerwerf (1950b), Hore, Mehrota & Hore (1991), Hore, Thakur *et al.* (1993), Hue & Étchécopar (1970), Inskipp & Inskipp (1991), Jayewardene (1989), Jeyarajasingam & Pearson (1999), Jior & Dhinda (1988), Kennedy *et al.* (2000), Khacher (1970), Law (1925), Lekagul & Round (1991), van Lynden (1951), MacKinnon & Philipps (1993, 2000), Madoc (1976), van Marle & Voous (1988), McClure (1998), Medway & Wells (1976), Merrie *et al.* (1986), Meyer de Schauensee (1984), Mienis (1980, 1994), Mukherjee (1973, 1995), Narayanan (1990), Oehler (1990), Paz (1987), duPont & Rabor (1973b), Porter *et al.* (1996), Rabor (1977), Riley (1938), Ripley & Rabor (1958), Roberts (1991), Roberts & Priddy (1965), Robson (2000a), Sen (1944), Shirihai (1996), Smythies (1986), Snow & Perrins (1998), Somadikarta (1973), Spittle (1952), Stepanyan (1990, 1995), Tehsin (1990, 1995), Ticehurst (1927), Tikader (1984), Tomlinson (2000), Voous (1951b), Wells (1999), Yahya & Yasmin (1991), Zhang Cizu *et al.* (1997), Zhao Zhengjie (1995), de Zylva (1973).

## 29. Javan Kingfisher

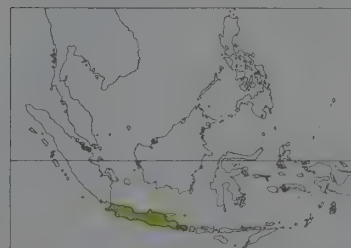
*Halcyon cyanoventris*

**French:** Martin-chasseur de Java      **German:** Javaliest      **Spanish:** Alción de Java  
**Other common names:** Blue-bellied Kingfisher

**Taxonomy.** *Halcyon cyanoventris* Vieillot, 1818, Java.

Forms a superspecies with *H. smyrnensis*, and sometimes considered conspecific, but the two overlap in range in W Java without hybridizing. Monotypic.

**Distribution.** Java and Bali.



**Descriptive notes.** 27 cm; female 93 g. Medium-sized, very dark-looking kingfisher. Both sexes have rich dark brown head, deep rufous collar and breast, dark purple body, turquoise-blue primary coverts, secondaries and tail; conspicuous white wing patch on bases of dark-tipped primaries striking in flight; bill red; iris dark brown, orbital skin red; legs and feet dark red. Juvenile duller, throat whitish, bill brownish-orange. **Voice.** Loud penetrating scream; loud "tjie-rie-rie-rie-rie"; repeated "tjeu-wii-ii" or "tschrii-ii".

**Habitat.** Uses variety of habitats, including pastures, fish ponds, paddyfields, dried

marshes, coastal scrub, mangrove, open dry forest, municipal gardens and parks, from the coast to about 1500 m. Usually avoids closed, humid forest except where this opened up by roads and paths.

**Food and Feeding.** Mainly insects taken on land, but also fish, frogs, freshwater shrimps, and larvae of water beetles (Dytiscidae). Flies down from a perch to catch prey on ground or at water's edge; sometimes hovers clumsily and plunges into water, but with little success.

**Breeding.** Lays in Feb-Sept. Nest dug by both pair-members, in bank of watercourse, earth mound, ditch, road cutting or earthen wall, in a sunny position; tunnel 1 m long, ending in nest-chamber. Clutch 3-5 eggs; no information on incubation and fledging periods.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Fairly common. Occurs in Baluran National Park and in Bali Barat National Park. Utilizes a diversity of habitats, but its range seems to be contracting; has not been recorded recently from some of its former haunts, e.g. Bogor (W Java). Reasons for apparent disappearance from some areas are not known and require investigation.

**Bibliography.** Andrew (1985, 1992), van Balen *et al.* (1988), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Hellebrekers & Hoogerwerf (1967), Holmes & Nash (1989), Hoogerwerf (1949a, 1949c, 1970), Hoogerwerf & Siccamo (1938), Inskipp *et al.* (1996), Jepson (1997), Knowles & Nitcher (1995), MacKinnon (1988), MacKinnon & Philipps (1993), Mason (1989), Rutgers & Norris (1977), Sargeant (1997), Whitten *et al.* (1997).

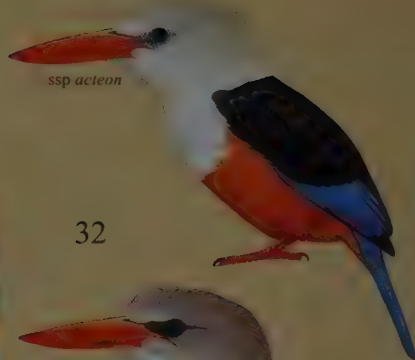


30



31

*ssp leucocephala*



*ssp acteon*

32



*ssp pallidiventr*



*ssp albiventris*



*ssp chelicuti*

33

*ssp prentissgrayi*

34

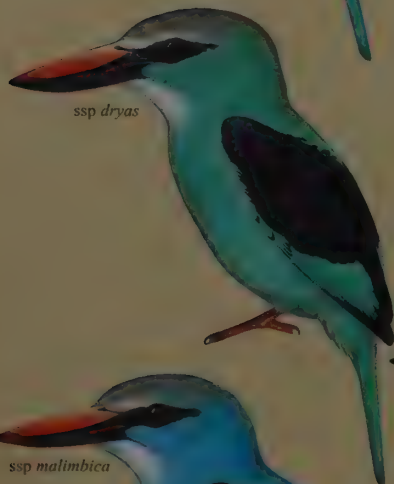


*ssp vociferans*



*ssp orientalis*

*ssp eremogiton*



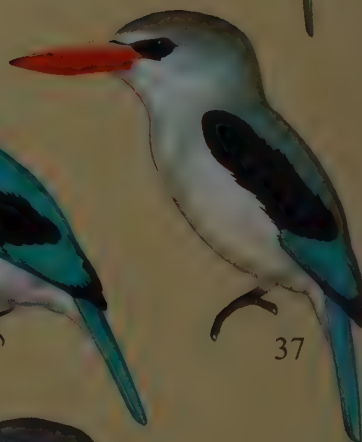
*ssp dryas*



*ssp cyanoleuca*

*ssp senegalensis*

36



37



*ssp malimbica*

35



*ssp torquata*



*ssp fuscopile*

PLATE 13

inches 5  
cm 13



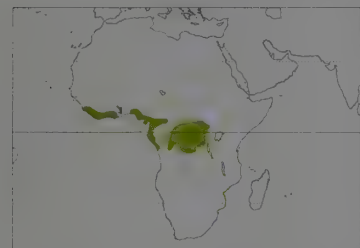
## 30. Chocolate-backed Kingfisher

### *Halcyon badia*

**French:** Martin-chasseur marron **German:** Kastanienliest **Spanish:** Alción Castaño

**Taxonomy.** *Halcyon (Cancrotophaga) badia* J. Verreaux and E. Verreaux, 1851, Gabon. Shows some affinities to *H. smyrnensis* and *H. cyanoventris*. Birds of Bioko I described as race *lopezi* and those from W Uganda as *budongensis*, but neither considered sufficiently distinct to merit recognition. Monotypic.

**Distribution.** Sierra Leone E to Ghana, and from S Nigeria, Bioko I (Fernando Póo) and S Cameroon E to extreme SW Central African Republic and S to Gabon and, marginally, N Angola (Cabinda, R Cuango), also Zaire (except N & SE) and extreme W Uganda (forests of Maragambo, Bwamba, Bugoma and Budongo).



**Descriptive notes.** 21 cm; male 54-65 g, female 47-65 g. Medium-sized, dumpy kingfisher. Both sexes have very dark chestnut head and upperparts, brilliant azure-blue on secondaries, rump and tail; pure white underparts and underwing; bill red; iris dark brown, narrow red orbital ring; legs and feet purple-red. Juvenile buffy scalloped breast, darker bill. **VOICE.** Single weak "pee", followed after 1 second by up to c. 17 long, fluty, pure notes lasting 5-7 seconds, series rising slightly in pitch at first and then falling, last 2 notes sometimes quieter, low-pitched and mournful; harsh, scolding screech as alarm.

**Habitat.** Primary and secondary lowland forest, from sea-level to 1500 m; not associated with aquatic habitats or human habitation, but requires arboreal termitaria for nesting. Occasionally found in savanna with remnant tracts of forest among abandoned farmland, or in second-growth forest.

**Food and Feeding.** Insects, mainly grasshoppers (Orthoptera) and beetles (Elateridae), also mantises (Mantodea), crickets (Grylloidea), cicadas (Cicadidae), bugs (Hemiptera), dragonflies (Odonata), ants (Formicidae), earwigs (Dermaptera), termites (Isoptera) and lepidopterous caterpillars; also spiders, and lizards. Perches quietly, high in a tree, for long periods, periodically flying down to catch prey on ground or to snatch flying insects in mid-air. Also perches low down near driver-ant columns, and feeds either on the ants themselves or on other insects disturbed by the column.

**Breeding.** Lays in Mar in Liberia and Nigeria, in Jun and Oct in Cameroon, around Nov on Bioko I, in Oct, Jan and Feb in Gabon, and in Sept in Zaire. Nest usually excavated in earthen termitarium of *Nasutitermes* hanging from a woody liane or sloping bough, 4-5 m above forest floor; tunnel 4-5 cm in diameter, dug horizontally from one side, and nest-chamber 25 cm long and 12 cm high, can occupy most of termitarium; arboreal ant nest and hollow in tree also used. Clutch 2-3 eggs; incubation by both sexes, period unknown; development of young seems quite rapid, at one nest a single young was fed 6 times a day and adults brought several prey items each time; fledging period undocumented.

**Movements.** Presumed to be sedentary.

**Status and Conservation.** Not globally threatened. Common in areas of suitable habitat; in Ghana and Nigeria it is uncommon, and confined to forest reserves and national parks. Occurs in Gola Forests Reserve, Sierra Leone, in Tai Forest National Park, Ivory Coast, in Korup National Park, Cameroon, in La Lopé National Park, Gabon, and in Kibale Forest National Park, Uganda. Continued destruction of forest is reducing its range.

**Bibliography.** Allport *et al.* (1989), Bannerman (1933, 1953), Britton (1980), Brosset (1974), Chapin (1939), Chappuis (1981), Christy & Clarke (1994), Clancey (1992), Colston & Curry-Lindahl (1986), Dean (2000), Dickerman *et al.* (1994), Dowsett (1989b), Dowsett & Dowsett-Lemaire (1991, 1993, 1997), Dowsett & Forbes-Watson (1993), Dowsett-Lemaire & Dowsett (1999, 2000), Elgood *et al.* (1994), Field (1999), Friedmann (1978), Friedmann & Williams (1971), Fry (1980a), Fry *et al.* (1988), Gartshore (1989), Gartshore *et al.* (1995), Gatter (1988, 1997), Gee & Heigham (1977), Germain *et al.* (1973), Grimes (1987), Hald-Mortensen (1971), Hockey (1997), Lippens & Wille (1976), Louette (1981b), Mackworth-Præd & Grant (1957, 1970), Pérez del Val (1996), Pinto (1983), Sargeant (1993), Serle (1950b), Serle *et al.* (1977), Short *et al.* (1990), Snow (1978), van Someren (1949), Taylor & Macdonald (1978), Traylor & Archer (1982), Walter *et al.* (1999), Wells (1968).

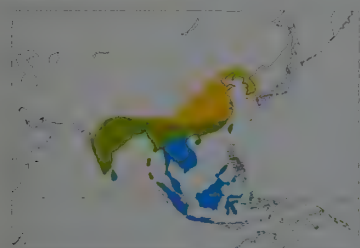
## 31. Black-capped Kingfisher

### *Halcyon pileata*

**French:** Martin-chasseur à coiffe noire **German:** Kapfenliest **Spanish:** Alción Capirotado  
**Other common names:** Black-capped Purple Kingfisher

**Taxonomy.** *Alcedo pileata* Boddaert, 1783, China. Forms a superspecies with *H. leucocephala*. Monotypic.

**Distribution.** India E to C, E & S China, Korea and Taiwan, S to Andaman and Nicobar Is, SW Myanmar, N Laos and Hainan. Winters S to Sri Lanka, Indochina, Malay Peninsula, Greater Sundas, Sulawesi and S Philippines.



**Descriptive notes.** 28 cm; 67-91 g. Medium-sized kingfisher. Both sexes have black head, white collar and throat, purple-black upperparts, pale orange-rufous underparts; white patch on primary bases conspicuous in flight; bill red; iris dark brown; legs and feet dark red. Juvenile duller, buffy collar, dusky scaling on breast, brownish-orange bill. **VOICE.** Ringing cackle, "kikikikikiki".

**Habitat.** In temperate regions inhabits deciduous forest near water, such as woodland riverbanks, and pools in forest streams. In the tropics and subtropics found both on the coast, in mangroves and on wooded seashores, and inland,

in creeks, lagoons, estuaries, rice fields, open cultivated land, *Nipa* palm groves, willow jungle, forest clearings, and streams in bamboo-forest; also in gardens. Mostly in lowlands, up to 1525 m; most common below 600 m in China.

**Food and Feeding.** In inland habitats, insects such as dragonflies and dragonfly nymphs (Odonata), water boatmen (Notonectidae), locusts and grasshoppers (Orthoptera), crickets (Grylloidea), leaf insects (Phasmatidae), beetles (Coleoptera), bees and wasps (Hymenoptera) are major food, but also takes a few frogs and reptiles; on the coast, mainly fish and crabs. Regularly uses a number of conspicuous perches, at height of 3-10 m, to survey surroundings, frequently changing position or perch; flies out to catch an insect in foliage or on the ground, or to take prey from water. Moves on to sandflats and mudflats at low tide to catch crabs.

**Breeding.** Lays from Apr in India; in Apr-May in Myanmar, in Jun in Korea, and in May-Jun in Hong-Kong. Nest at end of tunnel dug by both sexes in earth mound, cutting or streambank, occasionally in termitarium or old plaster-and-gravel wall; tunnel 50-100 cm long, 9-11 cm in diameter, ends in chamber 35 cm in diameter and 9-15 cm high. Clutch 4-5 eggs; no information on incubation and nestling periods. Recorded longevity 8 years.

**Movements.** Migratory in N of range. Breeders present in China and Korea May-Oct; non-breeding visitors Sept-Apr in Sri Lanka, Thailand, Indochina, and S to Greater Sundas (rare in Java) and Sulawesi (mainly in N). Resident or partial migrant in intervening regions, e.g. India, Bangladesh, and across to Hainan and Hong Kong; even where resident may make local post-breeding movements to the coast. Autumn passage in SW Thailand and in Peninsular Malaysia (at Fraser's Hill, in Pahang) from late Sept to late Nov, and spring passage Mar-Apr; many of these movements are at night and along well-established route, and individuals repeatedly recaptured over a number of years at same site. Shows strong fidelity to wintering territories; at Selangor, in S Malay Peninsula, some birds recaptured repeatedly at same place for up to 6 years in succession. Vagrants reported from periphery of its normal range, e.g. in Pakistan, Nepal, Vladivostok, and Japan (Hokkaido, Honshu, Ryukyu Is).

**Status and Conservation.** Not globally threatened. Has a wide distribution and uses broad range of habitats. Not well known, and no figures on population sizes; locally frequent or common in India; not uncommon in China, where probably common locally; in SE Asia, uncommon to fairly common breeder in Myanmar and N Laos, and fairly common to common non-breeding visitor throughout that region. Relative abundance in some of its wintering areas presumably reflects large breeding population, probably in inland China. In Peninsular Malaysia (Selangor), numbers wintering have declined since mid-1980's, and now found mainly on coast; oldest retrapped birds at Selangor were 8 years old, and annual mortality calculated at c. 50% a year.

**Bibliography.** Abdulali (1945), Aitken (1897), Ali (1996), Ali & Ripley (1983), Allen (1905a, 1905b), Amstutz (1973), Anon. (1956), Austin (1948), Baker (1934b), van Balen (1996), Betts (1957), Brazil (1991), Brown (1979), Burton (1978b), Butler (1899), Chen *et al.* (1995), Coates & Bishop (1997), Comber (1896), Daniels (1997), Deignan (1945), Dickinson *et al.* (1991), Duckworth *et al.* (1999), Etchécopar & Huc (1978), Fleming *et al.* (1976), Gibson-Hill (1949b), Gore (1968), Gore & Pyong-Oh (1971), Gregory-Smith (1996, 1997), Grimmett *et al.* (1998), Grubb *et al.* (1968), Harrison (1999), Harvey (1990), Henry (1998), Hewitt (1938), Holmes & Wood (1980), Hoogerwerf (1948a, 1948b), Indrawan, Collins *et al.* (1997), Inglis (1898, 1900, 1928), Jackson (1964), Jayewardene (1989, 1997), Jeyarajasingam & Pearson (1999), Jones (1908), Junge (1936), Kennedy *et al.* (2000), Kudo (1981), Kylänpää (1998), Lamsfus (1998), Lekagul & Round (1991), MacKinnon & Phillips (1993, 2000), van Marle & Voous (1988), McClure (1998), Medway & Wells (1976), Meyer de Schauensee (1984), Ogi *et al.* (1994), duPont & Rabot (1973a), Riley (1938), Robson (2000a), Savile (1909), Smythies (1986, 1999), Stepanyan (1990, 1995), Stevens (1904), Thompson (1966), Tikader (1984), Vidal (1897, 1898), Wells (1999), White & Bruce (1986), Zhang Cizu *et al.* (1997), Zhao Zhengjie (1995).

## 32. Grey-headed Kingfisher

### *Halcyon leucocephala*

**French:** Martin-chasseur à tête grise **German:** Graukopfliebt **Spanish:** Alción Cabeciblanco  
**Other common names:** Grey-hooded/Chestnut-bellied(!) Kingfisher

**Taxonomy.** *Alcedo leucocephala* P. L. S. Müller, 1776, Senegal.

Forms a superspecies with *H. pileata*. Proposed race *centralis*, described from Kenya and N Tanzania, now included within race *hyacinthina*. Five subspecies recognized.

**Subspecies and Distribution.**

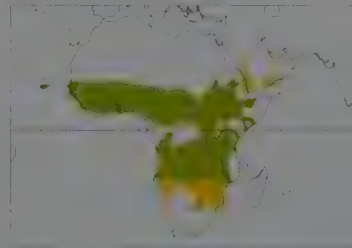
*H. l. aetonea* (Lesson, 1830) - Cape Verde Is (Brava, Fogo, Santiago).

*H. l. leucocephala* (P. L. S. Müller, 1776) - Senegambia E to Eritrea and Somalia, S to Gabon, NE Zaire, L Victoria basin and N Tanzania.

*H. l. semicaerulea* (J. F. Gmelin, 1788) - SW Arabia, from Mecca S to Yemen and E to Oman (Taqa); possibly winters in Somalia.

*H. l. hyacinthina* Reichenow, 1900 - SE Somalia, coastal Kenya and Tanzania (S to Dar es Salaam and W to Pare Mts and Kilosa).

*H. l. pallidiventris* Cabanis, 1880 - Zaire and Tanzania (except E) S to N Namibia and NE South Africa; S populations migrate N to Zaire, Tanzania, Uganda and Kenya.



**Descriptive notes.** 22 cm; 35-61 g, males average 42 g, females 43 g. Small to medium-sized kingfisher with reddish belly. Male nominate race grey head, black lores, black back and wing-coverts, bright blue wings, rump and tail; greyish-white breast, rufous-chestnut belly and vent; in flight underwing black, with primary bases white, coverts rufous-chestnut; bill red; iris dark brown; legs and feet red. Female slightly duller, rufous paler. Juvenile scaly head and breast, buffy belly. Race *aetonea* has head paler, blues darker, chestnut paler; *semicaerulea* shows slightly purer blues; *hyacinthina* wings and tail tinged violet; *pallidiventris* has belly and vent

paler. **VOICE.** Loud chattering trill, "trrrit-it-it-it"; loud "weep weep trrrr wooop", whistled "cheeo cheeo weecho-trrrr", chattering "dji-dji-dji-dji" or "chirr-r-r-r-r" falling in pitch, and twittering "ttrr", loud "tsi-tsi-tsi-tsi...", clear "tew-uuuuu", and descending "piuu piiu piiu".

**Habitat.** Woodland, thickets, thornbush, riparian trees along watercourses, bushy grassland, parkland and cultivated areas, from sea-level to 2400 m. Migrants use wider range of open habitats, including gardens and desert palms, but avoid thick forest or very arid regions.

On following pages: 33. Brown-hooded Kingfisher (*Halcyon albiventris*); 34. Striped Kingfisher (*Halcyon chelicuti*); 35. Blue-breasted Kingfisher (*Halcyon malimbica*); 36. Woodland Kingfisher (*Halcyon senegalensis*); 37. Mangrove Kingfisher (*Halcyon senegaloides*).



**Food and Feeding.** Mainly insects, particularly grasshoppers and locusts (Orthoptera), and also crickets (Grylloidea), mole-crickets (Gryllotalpidae), cockroaches (Blattodea), mantises (Mantodea), bugs (Hemiptera), ants (Formicidae), beetles (Coleoptera), and moths and caterpillars (including Sphingidae); also spiders, scorpions (Scorpiones) to 50 mm in length, slow-worms (Anguillae), small lizards; occasionally mice, frogs, fish, and nestling birds (*Merops*). Sits on a perch, scanning different areas in turn, and jerking its head up and down a few times, before flying down to catch prey. Most prey taken from ground, but some insects captured in flight; fish may be taken in low flight over the water. Small prey swallowed whole; larger ones are hit against perch, removing many of the legs, before being swallowed.

**Breeding.** Season late Jul-Dec in Cape Verde Is, from Feb-Mar in Ivory Coast, May-Oct in Senegal, Gambia and Mali, and Jan-Jun (dependent on latitude) in Nigeria; May-Jun in Sudan, Oct-Jun in Ethiopia; all months but mainly in wet season (Oct-Dec) in E Africa; lays Aug-Sept in Angola, Sept-Feb (mainly Oct-Nov) in Zambia, Oct-Nov and Feb in Malawi, Sept-Dec (mainly Oct-Nov) in Zimbabwe, and Oct-Nov in Natal. Monogamous; generally solitary breeder, and territorial, but 18 nests together at a sand quarry in Zambia. Paired birds sing from treetop, pivoting, and flicking wings open to show pattern, also circle together high above ground, calling continuously, then dive back to tree. Nest excavated in riverbank, road cutting, irrigation ditch, erosion gully, ground termarium, or roof of aardvark (*Orycteropus afer*) burrow, a horizontal tunnel 5 cm wide and 40-100 cm long, ending in nest-chamber 15 cm wide and 10 cm high; occasionally old tree hole used, including old nest of woodpecker (Picidae), rarely hole in stone wall. Clutch 2-6 eggs, mean 4; incubation period not documented; both sexes feed young, fledging period c. 21 days. Nests parasitized by Greater Honeyguide (*Indicator indicator*).

**Movements.** Timing and extent of movements vary regionally. Cape Verde population and perhaps some in equatorial Africa are resident; E African coastal race (*hyacinthina*) also resident, though some birds occasionally wander to Zanzibar and Pemba. Populations at higher latitudes exhibit more definite movements. Arabian breeders present Apr to mid-Dec, probably winter in Somalia. In Nigeria, S populations present near coast Nov-Apr, breed in dry season (Jan-Feb) and migrate N for wet season; N populations in desert-edge Sahel zone nest in wet season (Jul-Aug) and migrate S for dry; not known whether same individuals breed twice a year. Populations at middle latitudes have complex 3-stage migration: breed Mar-Jun, move to far N to moult in wet season (Jul-Aug), then migrate to far S for dry season, and finally return N to breeding grounds. In Nigeria, the peak of juvenile migration is 1-2 weeks later than that of adults. Ethiopian birds migrate S to E Africa, 2 individuals travelled 960 km to Uganda and 1750 km to Kenya, respectively. Some of these N populations migrate to S Africa. S population of *paludiventris* breeds in austral summer, then moves N in Apr-May to as far as C Zaire, Uganda and C Kenya, returning Aug-Sept, but some remain in dry season in the Zambezi Valley, Zambia and Malawi; one ringed in Malawi was recovered 1430 km away, in Zaire. Some S populations show 3-stage migration like those in N, breeding in N Zambia, moving S to arid Botswana and Namibia at peak of wet season, then moving N to equatorial non-breeding grounds; in years with above-average rainfall, more of these kingfishers migrate to S Africa and species is present farther S in arid areas.

**Status and Conservation.** Not globally threatened. Has wide distribution and uses a wide variety of open habitats. Generally common to fairly common throughout its range; a pair every 0.5-1 km along rivers in Nigeria; can be plentiful on migration. Some are killed while migrating by flying into buildings at night. In some areas, nests are not infrequently robbed by children.

**Bibliography.** Allport *et al.* (1989), Anon. (1998b), Archer & Goodman (1937-1961), Ash & Miskell (1983, 1998), Aspinwall (1984a), Attwell & Attwell (1990), Backhurst (1977), Bannerman (1953), Bannerman & Bannerman (1968), Barlow *et al.* (1997), Beaman & Madge (1998), Benson (1982), Benson & Benson (1977), Benson *et al.* (1971), Bouet (1961), Brooke (1984), Brooks *et al.* (1987), Browne (1981), Brunel (1958), Cave & Macdonald (1955), Chapin (1939), Cheke & Walsh (1996), Christy & Clarke (1994), Clancey (1971a, 1992, 1996), Cramp (1985), Curry-Lindahl (1960), Dean (1974), Dekeyser & Derivot (1966), Demeey & Fishpool (1991), Dowsett (1988), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgood, Fry & Dowsett (1973), Elgood, Heigham *et al.* (1994), Evans, M.I. (1994), Field (1999), Friedmann (1930a), Fry (1970b, 1980a), Fry *et al.* (1988), Gallagher & Rogers (1980), Garcia (1975), Gatter (1997), Gee & Heigham (1977), Ginn *et al.* (1989), Giraudoux *et al.* (1988), Gore (1990), Greig-Smith (1976), Grimes (1987), Grun & Schmitt (1991), Hammer (1976, 1980b), Harrison *et al.* (1997), Harwin (1984a), Hazevoet (1995), Heigham (1976), Herremans (1994), Hockey (1997), Hockey *et al.* (1989), Hollom *et al.* (1988), Jackson (1972), Jennings (1995), Jones (1980), Kemp (1974), Lack & Quicke (1978), Lewis & Pomeroy (1989), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Morel & Morel (1990), de Naurois (1969, 1983), Nikolaus (1987), Oatley (1982), Pakenham (1979), Penry (1994), Pinto (1983), Porter *et al.* (1996), Rands *et al.* (1987), de Ruiter (1998b), Salewski & Schmidt (2000), Serle (1939, 1950b, 1965), Serle *et al.* (1977), Short *et al.* (1990), Skinner (1968), Snow (1978), Snow & Perrins (1998), van Someren (1956), Wennrich (1982), Zimmerman *et al.* (1996).

## 33. Brown-hooded Kingfisher

### *Halcyon albiventris*

**French:** Martin-chasseur à tête brune **German:** Braunkopfliegt **Spanish:** Alción Cabecipardo  
**Other common names:** Brown-headed Kingfisher

**Taxonomy.** *Alcedo albiventris* Scopoli, 1786, Cape of Good Hope.

W populations described as a separate race, *hylophyla*, on basis of slightly darker coloration, but considered insufficiently distinct from *prentissgrayi*; population from S Somalia and NE Kenya described as race *erlangeri*, but apparently indistinguishable from *orientalis*. Four subspecies recognized.

#### **Subspecies and Distribution.**

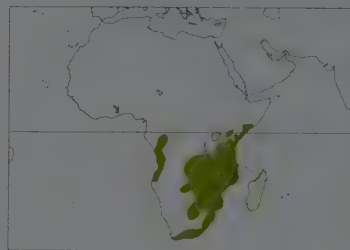
*H. a. prentissgrayi* Bowen, 1930 - E Gabon, S Congo, SW Zaire, W Angola and S Kenya. WC Tanzania to N Zambia.

*H. a. orientalis* W. K. H. Peters, 1868 - coastal lowlands from S Somalia to Mozambique, inland to Malawi, S Zambia, Zimbabwe and N Botswana.

*H. a. vociferans* Clancey, 1952 - E Botswana E to S Mozambique, S to Orange Free State and Natal.

*H. a. albiventris* (Scopoli, 1786) - Natal to SW Cape Province; migrates to S Zimbabwe.

**Descriptive notes.** 22 cm; male 48-53 g, female 54-58 g. Small to medium-sized kingfisher. Male nominate race dark-streaked brown head, pale supercilium, whitish collar streaked, blackish back and upperwing-coverts, contrasting turquoise wings, rump and tail; creamy below, streaked breast and flanks; bill red; iris dark brown; legs and feet red. Female like male, but darker crown, browner back, more streaky and tawny underparts. Juvenile duller, bill dark, distinguished from similar *H. leucocephala* by being streaked, not mottled, on head and breast. Race *vociferans* paler, crown and breast with lighter streaking, female may show plain white collar; *orientalis* smaller, paler, underparts unstreaked; *prentissgrayi* also smaller, crown less streaked, underparts more tawny. **Voice.** Loud descending "kieu ki-ki-ki-ki", weak trilled "tiiiui" or "ki-ti-ti-ti" singly or repeated up to 20 times in 17 seconds, drawn-out "pi-ee-ee, pi-ee-ee", also sharp "cheerit" alarm; also chuckle then



mm in length, millipedes (Sphaerotheriidae), molluscs, worms (Oligochaeta), and crabs; also small vertebrates, including frogs and tadpoles, lizards (Gekkonidae, Scincidae), snakes to 23 cm long, young birds (Sylviidae, Estrilidae), small rodents, rarely fish. Perches quietly on a branch or wire, looking around alertly; swoops down to prey on ground, not always alighting, then returns to perch, where larger items are battered before being swallowed head first. Will also snatch prey from foliage or tree trunks. Rare attempts at fishing seldom successful.

**Breeding.** Lays in Sept-Oct in SW Zaire and Angola; in Feb-Mar, Jun and Sept-Nov in Kenya and Tanzania; in Oct-Feb in Malawi and Zambia, in Sept-Dec (mainly Oct) in Zimbabwe and adjacent Mozambique, and in Sept-Apr (mainly Sept-Dec) in South Africa. Monogamous, solitary nester. Calls territorially, perched upright, wings held loosely and vibrating; pair-members display facing each other, singing continuously, the body pivoting and bobbing, tail fanned and raised, wings periodically flicked open; courtship feeding with a scorpion recorded. Nest-tunnel dug 1.5 m above ground in road cutting, streambank or gully, tunnel 1 m long with nest-chamber at end, entrance hole 6 cm in diameter and sometimes overhung with vegetation; 2 nests found in Zaire in old woodpecker (Picidae) holes, and in S Africa may nest in hole in colony of sand martins (*Riparia*) or bee-eaters (*Merops*). Clutch 2-5 eggs, rarely 6, mean 3.7 in S Africa, 3-4 in E Africa; incubation period c. 14 days; female feeds young twice as much as does male, well-grown young void faeces from tunnel entrance; fledging period c. 21 days.

**Movements.** Most populations appear to be sedentary. South African race *albiventris* occurs in S Zimbabwe in austral winter, mid-Apr to, possibly, Aug, but little evidence of seasonality in most of South Africa; seasonal changes in numbers also noted elsewhere, e.g. Malawi, and in Kenya present only Oct-May in Tsavo National Park. Probably migratory in NE of range, in Somalia. Ringing recoveries show movements of 18 km and 32 km.

**Status and Conservation.** Not globally threatened. Widespread, and common or, at least, locally common in many parts of its range. This species' wide distribution and its use of open habitats mean that populations are likely to be stable. Now often found in suburban development of previously treeless grassland; has expanded its range in S Karoo and SW Cape Province. Has bred successfully in captivity.

**Bibliography.** Anon. (1998b), Argyle (1971), Ash & Miskell (1983, 1998), Bannerman (1953), Barnard *et al.* (1984), Beesley (1973), Benson (1982), Benson & Benson (1977, 1979), Benson *et al.* (1971), Bouet (1961), Bower & Crawford (1983), Britton (1980), Chapin (1939), Clancey (1959c, 1964a, 1971a, 1976, 1986, 1992, 1996), Dean (1971, 1974, 2000), Dekeyser & Derivot (1966), Desman (1998), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Fitz-Gerald (1997), Friedmann (1930a), Fry (1980a), Fry *et al.* (1988), Ginn *et al.* (1989), Haagner (1997), Hammer (1976, 1980b), Harrison *et al.* (1997), Harwin (1984a), Hockey (1997), Hockey *et al.* (1989), Jackson, F.J. & Selater (1938), Jackson, H.D. (1972), Kemp (1974), Kyle (1997), Lewis & Pomeroy (1989), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Martin (1996), Medland (1989), Oehler (1990), Parker (1999), Penry (1981, 1994), Pinto (1983), Sargeant (1993), Short *et al.* (1990), Snow (1978), van Someren (1956), Tree (1963c), Wickler & Seibt (1984), Wilson, J. (1993), Zimmerman *et al.* (1996).

## 34. Striped Kingfisher

### *Halcyon chelicuti*

**French:** Martin-chasseur strié

**German:** Streifenliet

**Spanish:** Alción Estriado

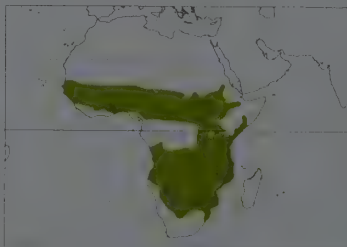
**Taxonomy.** *Alcedo* [sic] *Chelicuti* Stanley, 1814, Chelicut, Ethiopia.

Previously placed in monospecific genus *Chelicutia*. Races intergrade; a certain amount of geographical variation in dorsal coloration does not seem sufficient to warrant recognition of proposed races *hylobia* (W Zaire, NW Angola) and *damarensis* (S Angola E to Mozambique and Transvaal). Two subspecies currently recognized.

#### **Subspecies and Distribution.**

*H. c. eremogiton* Hartert, 1921 - Sahel zone from SC Mali and N Nigeria E to Sudan.

*H. c. chelicuti* (Stanley, 1814) - S Mauritania to NW & S Somalia, S to NE Namibia, Botswana and N & NE South Africa (Natal).



**Descriptive notes.** 17 cm; male 30-41 g, female 37-50 g. A small woodland kingfisher. Male nominate race white line above forehead, heavily brown-streaked crown, black eyband, whitish collar, dark brown mantle, blue back and rump, blue on wings, greenish tail; breast streaked, flanks heavily streaked; underwing with broad black subterminal band on flight-feathers; bill dark, red base of lower mandible; iris dark brown; legs and feet dull red. Female less streaky, crown browner, no black subterminal band on underwing. Juvenile only slight blue in wing and tail, buffier flanks and belly, dark barring on breast. Race *eremogiton*

crown and mantle grey-brown, wing-coverts paler, underparts hardly streaked. **Voice.** Loud, high-pitched "keep-ki-rrrrr" or "pee-hee", 1-2 seconds long, repeated up to 10 times, less disyllabic in E than in W or S; long trill warns nestlings of danger, much quieter version in courtship feeding or during nest-relief; harsh rasp during attacks on predators or intruders into territory.

**Habitat.** Woodland, wooded grassland, and thornbush, from sea-level to 2300 m; avoids forest, and found only in the largest clearings. Occurs in farmland with trees and stockyards, but not in heavily cultivated areas; moves into more arid regions than frequented by other African *Halcyon* species. Distribution often discontinuous, suggesting habitat preferences which are not fully understood.

**Food and Feeding.** Insects, mainly grasshoppers (Orthoptera), also beetles (Coleoptera), larvae, butterflies, moths and caterpillars, mantises (Mantodea), cicadas (Cicadidae), termites (Isoptera);



occasionally small lizards, snakes and rodents. In N Ghana, grasshoppers comprised 62% of prey, beetles 19%, larvae 12% and butterflies 6%. Watches for prey from a perch, usually 2.5-3.5 m high in N Ghana, occasionally moving position; swoops down to ground and carries prey back to perch; in one study, 3-17 swoops per 100 minutes, with 80% success. Small items swallowed whole, large ones knocked against perch before being swallowed. Flying termites and moths are caught on the wing.

**Breeding.** Lays in Jun-Sept in Senegal, in Jun-Jul in Gambia, in Sept-Oct in Mali, in Mar-Apr in Nigeria, and in Jan-Oct in Ethiopia; all months in E Africa; in Apr-Sept in S Zaire, in Sept-Feb but mainly Sept-Oct in Zimbabwe; in Aug-Nov and Mar in Malawi; in Oct-Nov in Zambia, and in Sept-Feb in South Africa; double brooded. In Kenya, 20% of territories had 2 males, both mated with the female and helped rear young. Strongly territorial, birds call from treetops, as a duet, starting before dawn and continuing at intervals until afternoon, and chorus of responding callers heard particularly towards dusk; in display, pair-members face each other on treetop, erect, tail cocked to expose blue rump, flicking wings open and shut, singing repeatedly; wing-flicks may start in unison but finish by alternating; male courtship-feeds female, which tears parts of prey from his bill. Nest in old hole made by barbet (Capitonidae) or woodpecker (Picidae), 1-10 m up in tree; occasionally uses nestbox, hollow post, hole under eaves, old nest of swallow (Hirundinidae), or natural tree hollow; entrance 5 cm in diameter, eggs laid c. 20 cm from entrance. One territory was 3 ha in size, containing 100 mature trees to 12 m high. Clutch 3-5 eggs in tropics, 2-6 (mean 3.4) in South Africa; incubation by both sexes during the day, only by female at night; no information on incubation and fledging periods; second clutch laid in same or different nest 1 month after first brood fledges. In Kenya, c. 25% of nests are parasitized by honeyguides (*Indicator*).

**Movements.** Most populations apparently sedentary, but local movements reported from several localities. No evidence for seasonal movement in South Africa, but some indication of irregular movements; after drought in Kalahari, this species was abundant along roads in E hardveld of Botswana.

**Status and Conservation.** Not globally threatened. Widely distributed, and common to fairly common in most of range. Able to thrive in quite open habitat and around cultivated lands, provided these are not too extensive; distribution often somewhat patchy, however, and adjacent territories probably not contiguous; absent from some apparently suitable areas; further study needed of its exact habitat requirements. Some mortality reported after spraying of DDT against tsetse flies (*Glossina*) in Zimbabwe.

**Bibliography.** Archer & Goodman (1937-1961), Ash & Miskell (1983, 1998), Bannerman (1953), Barlow *et al.* (1997), Beesley (1973), Benson (1982), Benson & Benson (1977), Benson *et al.* (1971), Bouet (1961), Bowen (1978), Britton (1980), Brunel (1958), Cave & Macdonald (1955), Cheke & Walsh (1996), Clancey (1964a, 1971a, 1991, 1992, 1996), Curry-Lindahl (1960), Dean (1971, 1974, 2000), Douthwaite (1995), Dowsett (1988), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Elgood, Fry & Dowsett (1973), Elgood, Heigham *et al.* (1994), Field (1999), Friedmann (1930a), Fry (1980a), Fry *et al.* (1988), Garcia (1975), Gatter (1988, 1997), Germain *et al.* (1973), Ginn *et al.* (1989), Giraudoux *et al.* (1988), Godwin (1987), Gore (1990), Greig-Smith (1978b), Grimes (1987), Hamner (1976, 1980b), Hamner & Godwin (1987), Harrison (1997), Harwin (1984a), Hockey (1997), Hoesch (1933b), Howells (1970), Jackson & Sclater (1938), Johnson (1995), Kemp (1974), Lamarche (1988), Lewis & Pomeroy (1989), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Medland (1993), Millar (1908), Morel & Morel (1990), Nikolaus (1987), Pakenham (1979), Parker (1999), Penny (1994), Pinto (1983), Quantrill & Quantrill (1998), Reyner (1980b), Rodwell (1996), Sargeant (1993), Schels & Lavoyer (1987), Schmidt (1993), Serle *et al.* (1977), Short *et al.* (1990), Snow (1978), Steyn (1970), Stoneham (1930), Tarboton *et al.* (1987), Thiollay (1973a), Urban & Brown (1971), Zimmerman *et al.* (1996).

## 35. Blue-breasted Kingfisher

### *Halcyon malimbica*

**French:** Martin-chasseur à poitrine bleue **German:** Zügelstiebt **Spanish:** Alción Pechiazul  
**Other common names:** Black-winged Kingfisher

**Taxonomy.** *Alcedo Malimbica* Shaw, 1811, Malimba, Zaire.

Population from Senegal, described as race *fortis*, now included in *torquata*; proposed race *prenticei*, from S Sudan, NE Zaire and Uganda, inseparable from nominate. Four subspecies recognized.

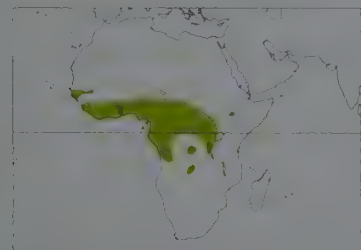
**Subspecies and Distribution.**

*H. m. torquata* Swainson, 1837 - Senegal E to SW Mali and S to N Guinea.

*H. m. forbesi* Sharpe, 1892 - Sierra Leone E to S Nigeria, Bioko I (Fernando Póo) and SW Cameroon.

*H. m. dryas* Hartlaub, 1854 - Principe I and, at least formerly, São Tomé I.

*H. m. malimbica* (Shaw, 1811) - S Cameroon E to SW Sudan, W Uganda and NW Tanzania, and S to N Angola and NW Zambia; probably this race in SE Ethiopia.



**Descriptive notes.** 25 cm; male 64-94 g (*torquata*), female 70-93 g (*torquata*), sexes combined 108-121 g (*malimbica*), 110-130 g (*dryas*). Medium-sized kingfisher with blue and black plumage. Both sexes nominate race grey-brown forecrown, white supraloral line, black eyeband, blue head side, hindneck and mantle; black back, scapulars and wing-coverts, blue rump and tail, blue bases of primaries and secondaries; white throat, blue breast, white belly; red upper mandible, black lower mandible; iris dark brown; legs and feet dark red. Juvenile crown and breast washed greenish, underparts buffy. Race *forbesi* paler blue, more

greenish; *torquata* shows blues even paler and more greenish; *dryas* larger, paler with obvious green wash, crown ash-brown, entire underparts greenish-blue. Voice. Single note, pause for a second, then series of piping whistles, at first short and clipped, becoming longer and more emphatic, "chhu pu-pu-pu pu ku ku"; alarm a raucous "tchup tchup-tchup-tchup" for 1-5 seconds. **Habitat.** Rainforest, gallery forest along watercourses in savanna, secondary forest, mangroves, riverine woodland, and thick savanna woodland dominated by *Anogeissus leiocarpus*, also isolated patches of woodland in savanna; from sea-level to 1800 m.

**Food and Feeding.** Mainly invertebrates, including cockroaches (Blattodea), grasshoppers (Orthoptera), termites (Isoptera), wasps (Hymenoptera), beetles (Coleoptera), mantises (Mantodea), spiders, millipedes (Diplopoda), whip-scorpions (Uropygi), crabs and molluscs (Gastropoda, *Columna*); also fish, such as mud-skippers (*Pariophthalmus*), and frogs and toads, lizards, birds, mice; also fruits of oil palm (*Elaeis guineensis*). In Ivory Coast, 70% of diet was arthropods, 10% insect larvae, 20% unidentified, with small percentage of vertebrates. Searches for prey from a perch low down near a stream or wet ground, or from a large branch, up to 5 m high in forest; flies down to snatch prey, sometimes remaining on ground for a short time to beat it on hard substrate, or returning to perch to eat it there before swallowing. May fly out to snatch an insect from foliage.

Sometimes joins mixed bird flocks following columns of driver ants (*Dorylus*) to feed on the fleeing insects and small vertebrates.

**Breeding.** Lays in Aug-Sept in Guinea-Bissau, in Mar-Apr in Ghana, in Jan-Jun in Nigeria, in Aug in Cameroon, in Dec-Jun in Gabon, in Oct-Dec on Principe and in Apr in Uganda. Displays by calling from near top of a tree, pointing bill up, and rapidly opening and closing wings and jerking up tail; male similar posture to courtship-feed female. Nest-tunnel dug into arboreal termitarium, usually of *Microcerotermes*, at height of 6-10 m; once recorded using hole 5 m up in dead tree. Clutch 2-4 eggs; no information on incubation and fledging periods. Some nests raided by chimpanzees (*Pan troglodytes*).

**Movements.** Largely resident. Some range reduction in dry season, e.g. in Nigeria all N records are from wet season in May-Sept; mainly a wet-season visitor Apr-Jul to Accra Plain forest outliers in Ghana; in Gambia widespread breeder in woodland savanna during the summer rains, but moves to denser riverine woodland of upper R Gambia in dry season.

**Status and Conservation.** Not globally threatened. Widespread in W & C Africa, but most common in rainforest and mangroves, becoming more localized and less common in drier habitats; thus, it may decline with habitat loss. Now very rare or extinct on São Tomé, and small population in Burundi likely to be extinct owing to forest clearance. Population levels difficult to assess; this species is wary in most areas, disappearing into forest with an alarm call when disturbed.

**Bibliography.** Allport *et al.* (1989), Anon. (1995b), Ash (1992), Aspinwall & Beel (1998), Atkinson *et al.* (1994), Bannerman (1933, 1953), Barlow *et al.* (1997), Becroft & Wilkinson (1983), Benson *et al.* (1971), Bouet (1961), Brosset & Égard (1986), de Castro & de Castro (1990), Chapin (1939), Cheke & Walsh (1996), Christy & Clarke (1994, 1998), Clancey (1992), Colston & Curry-Lindahl (1986), Dean (2000), Dekeyser & Derivot (1966), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Dowsett-Lemaire & Dowsett (1999, 2000), Elgood *et al.* (1994), Field (1999), Friedmann (1978), Friedmann & Williams (1969, 1971), Fry (1980a), Fry *et al.* (1988), Gartshore (1989), Gartshore *et al.* (1995), Gatter (1988, 1997), Gaugris *et al.* (1981), Gee & Heigham (1977), Germain *et al.* (1973), Giraudoux *et al.* (1988), Gore (1990), Greig-Smith (1976), Grimes (1987), Harwin (1984a), Hockey (1997), Jones & Tye (1988), Leonard (1998a), Mackworth-Præd & Grant (1957, 1962, 1970), Morel & Morel (1990), de Naurois (1980, 1994), Okia (1976), Pinto (1983), Rand (1951), Rand *et al.* (1959), Rodwell (1996), Serle (1965, 1981), Serle *et al.* (1977), Short *et al.* (1990), Snow (1950, 1978), van Someren (1949), Thiollay (1973a), T aylor & Parellis (1967), Wareman (1987).

## 36. Woodland Kingfisher

### *Halcyon senegalensis*

**French:** Martin-chasseur du Sénégal **German:** Senegalliest **Spanish:** Alción Senegalés  
**Other common names:** Angola/Red-and-black-billed/Senegal Kingfisher, Angolan Woodland Kingfisher

**Taxonomy.** *Alcedo senegalensis* Linnaeus, 1766, Senegal.

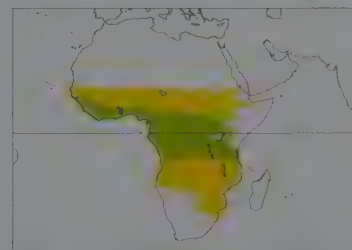
Forms a superspecies with *H. senegaloides*. S race *cyanoleuca* has in past been treated as a full species. Race *fuscipile* sometimes merged with nominate. Three subspecies currently recognized.

**Subspecies and Distribution.**

*H. s. senegalensis* (Linnaeus, 1766) - Senegambia E to Ethiopia and S to W Kenya, NW Tanzania, Rwanda and Burundi.

*H. s. fuscipile* Reichenow, 1906 - Sierra Leone to S Nigeria, Bioko I (Fernando Póo) and Congo Basin.

*H. s. cyanoleuca* (Vieillot, 1818) - NW Tanzania S to Angola, Botswana and NE South Africa.



**Descriptive notes.** 23 cm; male 41-60 g, female 55-64 g, in S Africa 60-81 g. Medium-sized kingfisher. Both sexes nominate race greyish crown, black lores, blue hindneck, upperparts and tail, black wings with blue bases of flight-feathers; underparts greyish-white; red upper mandible, black lower mandible; iris dark brown; legs and feet reddish-black. Distinguished from *H. malimbica* by blue back, from similar *H. senegaloides* by black lower mandible. Juvenile buff wash with fine black barring on face and underparts, blackish bill. Race *fuscipile* smaller, darker, crown dark brown-grey, breast and mantle greyer; *cyanoleuca*

larger, crown paler, black wedge behind eye, some birds in Malawi with red patches on lower mandible. Voice. Single sharp "tiu" followed by loud fast trill lasting 2-3 seconds, slowing and falling slightly towards end, "ttrrrrrrrrr", usually repeated 10 times (up to 40) at intervals of 5-10 seconds, often continual "ttrrrrr-ttrrrrr-ttrrrrr-ttrrrrr" by pair flying around territory boundaries; alarm harsh screech, "kee-kee-kee-kee-kee"; greeting call "chowaa-rr... chowaa-rr", at the nest soft mellow "chirr-chirr", and "ki-kaw" squawk.

**Habitat.** Woodland, riverine forest, wooded areas around human dwellings, and forest clearings and edges; in savanna avoids closed cover, preferring open woodland, farmland, parks and large gardens; in S Africa, particularly common in riverine woodland where the grass understorey is heavily grazed. From sea-level to 1500 m, occasionally to 2000 m.

**Food and Feeding.** Insects, mainly grasshoppers and locusts (Orthoptera, Acrididae), beetles (Buprestidae, Carabidae, Cerambycidae, Cetonidae, Cicadellidae, Tenebrionidae), and also dragonflies (Odonata), cicadas (Cicadidae), cockroaches (Blattodea), mantises (Mantodea), moths and butterflies, larvae, ants (Formicidae) and termites (Isoptera); other arthropods including scorpions (Scorpiones), centipedes (Chilopoda), millipedes (Diplopoda); also shrimps and crabs, fish, frogs, lizards (Agamidae), snakes, small passerine birds (*Lonchura*, *Quelea*), and small mammals (Muridae). In N Ghana, grasshoppers comprised 90% of diet, and 59% of dives were successful; estimated food intake 26 grasshoppers per day. Spends much time perched in semi-shade, with occasional head-bobbing or tail-wagging, scanning for food; average height of perch above ground 2-6 m; swoops down to catch item on or near ground, then carries it back to perch. From a high perch gently spirals down until 3 m above ground, then dives on prey; occasionally flies horizontally from perch and briefly hovers before diving on prey; will also plunge into shallow water for fish. Large food items are held crosswise in bill, and bashed on perch before being swallowed. Alate termites are caught in flight.

**Breeding.** Lays in Mar-Sept, possibly also Oct, and Dec in N tropics, in Aug-Feb in Zaire, in Nov-Feb in Rwanda, in Nov-Dec in Zambia, in Dec-Jan in Malawi, in Nov-Jan in Zimbabwe and Mozambique, and in Oct-Mar in South Africa; sometimes double-brooded. Strongly territorial, chases off other hole-nesting birds, and raptors and humans. Display from tall tree, trilling with bill up and half-open, suddenly opening wings wide and pivoting body from side to side, display lasting 1-2 (up to 7) seconds, can be repeated 15 times, in intense display tail fanned and cocked; pair-members usually face each other and sing in duet, spreading wings, sometimes moving to show front and rear

of wings alternately; circling display-flight 15-20 m above ground with constant trilling calls may be territorial or for courtship; in courtship feeding female sits motionless, hunched, while male brings food, sometimes they touch bills without transferring food. Nest 1.5-9 m (average 5 m) above ground, generally in tree hole, often old nest of barbet (Capitonidae), woodpecker (Picidae), starling (Sturnidae) or *H. albiventris*, occasionally in nestbox, under house eaves, in arboreal termite nest, or in nest of Little Swift (*Apus affinis*); on rare occasions makes own nest-hollow, by flying at tree trunk and striking it with the bill; entrance hole 4-6 cm in diameter, nest-cavity 20-25 cm deep; same nest-hole occasionally used for up to 4 years. Clutch 2-4 eggs, usually 3; sometimes replacement laid if first clutch lost; both sexes incubate during day, but only female at night, incubation period 13-14 days; young fed by both parents, with a peak of feeding in early morning and mid-afternoon, nestling period 15-24 days; juveniles remain with adults for 5 weeks post-fledging.

**Movements.** Populations in equatorial forest (*fuscipile*) sedentary; savanna populations also sedentary to about 8° N & S of equator, beyond which they become progressively more migratory. In Nigeria resident in S forest and savannas, and visits N savannas (N of 9-10° N) from Apr-May to Nov, the Sahelian savannas in Jun-Sept, and to 17° N in Chad and Mali from Jul-Aug to Oct. In S Africa a breeding migrant from Oct-Nov to Apr, spending austral winter in equatorial Africa, and part of population crosses L Victoria Basin to winter in Sudan; on the central plateau in Zimbabwe only a passage migrant, in Nov and Apr. Migrates at night, solitary or in loose groups.

**Status and Conservation.** Not globally threatened. Widespread and common in many parts of its range. Is able to breed in cleared areas, provided some large trees remain. Migrants are often killed at windows at night. Has bred successfully in captivity.

**Bibliography.** Allport *et al.* (1989), Anon. (1988b), Bannerman (1953), Barlow *et al.* (1997), Benson (1944, 1982), Benson & Benson (1948, 1977), Benson *et al.* (1971), Bouet (1961), Cave & Macdonald (1955), Chapin (1939), Cheke & Walsh (1996), Christy & Clarke (1994), Clancey (1964a, 1971a, 1992, 1996), Colston & Curry-Lindahl (1986), Curry-Lindahl (1960), Dekeyser & Derivot (1966), Dowsett (1988), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Elgood, Fry & Dowsett (1973), Elgood, Heigham *et al.* (1994), Field (1999), Friedmann & Williams (1971), Fry (1980a, 1983b), Fry *et al.* (1988), Gartshore (1989), Gartshore *et al.* (1995), Gatter (1988, 1997), Gee & Heigham (1977), Germain *et al.* (1973), Ginn *et al.* (1989), Giraudoux *et al.* (1988), Gore (1990), Greig-Smith (1976, 1978a, 1979), Grimes (1987), Hanmer (1976, 1980b, 1983, 1984, 1989a, 1990), Harrison *et al.* (1997), Harwin (1984a), Heigham (1976), Herremans (1994), Hockey (1997), Jackson, D. (1968), Jackson, F.J. & Selater (1938), Kemp (1974), Laing & Laing (1983), Lamarche (1988), Lewis & Pomeroy (1989), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Mann (1953), Medland (1993), Meintjies (1943), Milstein (1962, 1983), Morel & Morel (1990), Nikolaus (1987), O'Sharkey (1978), Okia (1976), Penry (1994), Pérez del Val (1996), Pérez del Val *et al.* (1997), Pinto (1983), Rand (1951), Rand *et al.* (1959), Robinson (1970), Rodwell *et al.* (1996), Saunders (1973), Serle (1965), Serle *et al.* (1977), Sharp (1987), Short *et al.* (1990), Snow (1978), Thiollay (1973a, 1985a), Trautmann & Cullen (1983), Traylor (1960a), Ward, B.S. (1971), Wennrich (1982), Young (1946), Zimmerman *et al.* (1996).

37. Mangrove Kingfisher

*Halcyon senegaloides*

**French:** Martin-chasseur des mangroves    **German:** Mangroveliest    **Spanish:** Alción de Manglar  
**Other common names:** African Mangrove Kingfisher

**Taxonomy.** *Halcyon Senegaloides* A. Smith, 1834, near Port Natal, South Africa.  
Forms a superspecies with *H. senegalensis*. N populations sometimes considered to form a distinct race, *ranivorus*, but differences seem insufficient to warrant subspecific separation. Monotypic.

**Distribution.** SC Somalia (middle to lower Shabeelle Valley) S along coast, including offshore islands, to E South Africa (R Great Kei); generally within 20 km of coast, but 150 km inland on R Juba (Somalia), and on R Zambezi to Sena (Mozambique); inland records from Kruger National Park and elsewhere in South Africa not accepted.



**Descriptive notes.** 22 cm; 57-66 g. Both sexes grey-brown crown, black lores, greyish ear-coverts and hindneck, blue upperparts and tail, black wings with blue bases of flight-feathers; underparts greyish-white with buff wash; bill red, sometimes with dusky tip to lower mandible; iris dark brown; legs and feet dark grey-brown. Distinguished from very similar *H. senegalensis* by all-red bill, black patch at carpal joint of wing, also lacks black mark behind eye shown by S race *cyanoleuca* of that species. Juvenile blues duller, breast and flanks more buffy with fine barring, bill dark brown. **VOICE.** Raucous "tchi, tchi, tcha, tcha-tch-ch-ch" lasting 6-7

seconds, accelerating into slightly descending trill; "cling-cling-cling-cling..." at nest.

**Habitat.** Low-lying woodland and wooded rivers in open country, thornveld, deciduous and evergreen forest, city parks, fish ponds and gardens; wooded estuaries and mangroves in non-breeding season.

**Food and Feeding.** Crabs and prawns, fish, lizards, and insects. Perches quietly in a tree, flying to ground or water when prey sighted. A more frequent and efficient fisher than *H. senegalensis*, and takes quite large fish.

**Breeding.** Lays in Oct in Kenya, in Dec in Tanzania (Pemba I), and in Oct-Jan in South Africa. Treetop wing-spreading display like that of *H. senegalensis*. Nest in living or dead tree, sometimes old hole of barbet (Capitonidae) or woodpecker (Picidae), or in riverbank, possibly also in arboreal termitarium; a nest-tunnel in the side of a clay pit was 1 m long; nest may be reused for many years. Clutch 3 eggs; both parents feed young; no information on incubation and nestling periods.

**Movements.** Partial migrant; most leave the coast and mangroves in Sept-Oct and move inland to breed, return to coast in Feb-Mar. In South Africa, migrates from summer breeding grounds in the Transkei to coastal wintering grounds in Natal. Resident on Pemba I and Tumbatu I, but breeding visitor to Zanzibar Sept-Jan.

**Status and Conservation.** Not globally threatened. Has a wide distribution, in a range of habitats. Common to locally common in most of range; uncommon and rather local in Somalia. South African population is small, isolated and threatened by loss of habitat, could be considered vulnerable; occurs in Mtunzini and Umlalazi Nature Reserve, South Africa. Some birds, mainly juveniles, are killed by hitting wires and buildings while migrating.

**Bibliography.** Ash & Miskell (1983, 1998), Bell (1960), Bennun & Njoroge (1999), Benson (1982), Berruti *et al.* (1994), Britton (1980), Brooke (1984), Brown & Britton (1980), Clancey (1964a, 1965b, 1984c, 1985, 1992, 1996), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Erdal (1947), Fry (1980a, 1983b), Fry *et al.* (1988), Ginn *et al.* (1989), Hanmer (1976), Harrison *et al.* (1997), Harwin (1984a, 1984b), Hockey (1997), Jackson & Selater (1938), Jonsson (1965), Lewis & Pomeroy (1989), Mackworth-Praed & Grant (1957, 1962), Maclean (1993), Newman (1996), Pakenham (1979), Parker (1999), Pike (1966), Short *et al.* (1990), Siegfried *et al.* (1976), Sinclair, I. & Davidson (1995), Sinclair, J.C. (1987), Snow (1978), Tomlinson (2000), Turkington (1984), Zimmerman *et al.* (1996).









## Genus *TODIRAMPHUS* Lesson, 1827

### 38. Blue-black Kingfisher

#### *Todiramphus nigrocyaneus*

**French:** Martin-chasseur bleu-noir **German:** Dunkelläst **Spanish:** Alción Oscuro  
**Other common names:** Black-sided Kingfisher

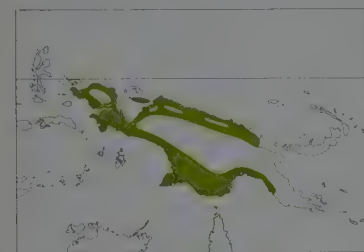
**Taxonomy.** *Halecyon nigrocyanea* Wallace, 1862, Manokwari, New Guinea. Genus often merged into *Halecyon*. Races very distinctive, and have on occasion been suggested to be separate species; however, intermediates have been found in areas of overlap, between nominate and *quadricolor* (on shores of Geelvink Bay) and nominate and *stictolaemus* (Merakue to R Fly), while ecology and vocalizations appear very similar, all together indicating that the three are probably conspecific. Three subspecies recognized.

#### **Subspecies and Distribution.**

*T. n. nigrocyaneus* (Wallace, 1862) - W Papuan Is (Batanta, Salawati) E to Geelvink Bay in N and to Princess Marianne Strait in S.

*T. n. quadricolor* (Oustalet, 1880) - Yapen I to Madang and Astrolabe Bay.

*T. n. stictolaemus* (Salvadori, 1876) - Koerik District and R Fly E to Mt Cameron (W Owen Stanley Range).



**Descriptive notes.** 23 cm; male 51-54 g, female 55-57 g. Medium-sized kingfisher with dark blue crown, paler blue supercilium, black mantle, pale blue back becoming darker on rump and tail. Male of nominate race has white chin and throat and white breast spot, blue breastband and belly; bill black, paler culmen; iris dark-brown; legs and feet greyish-black. Female white below but for blue breastband. Juvenile male duller, buffish fringes above, buffy below with dark orange breastband and flanks; juvenile female paler below, still with rufous breastband. Race *quadricolor* male blue chestband but chestnut belly; *stictolaemus* male

largely blue underparts, black mottling on white throat, entirely blue belly. **Voice.** Two ascending notes and short descending trill, lasting 3 seconds; female a repeated, piercing "cheez".

**Habitat.** Lowland to hill forest near streams, swamps and ponds, at up to 600 m; also flooded *Melaleuca* forest, occasionally eucalypt (*Eucalyptus*) forest, thickets by creeks and coastal village gardens.

**Food and Feeding.** Little known; crabs, fish and lizards recorded as prey. Perches high in the canopy or low over water; evidently takes prey both from land and from water.

**Breeding.** No information.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Data-deficient. Reportedly common in W of its range (Irian Jaya), becoming scarcer farther E (Papua New Guinea). Vulnerable to clearance of wet lowland forest. More information on this species' status and biology is urgently required.

**Bibliography.** Andrew (1992), Beehler *et al.* (1986), Bellchambers *et al.* (1994), Coates (1985), Eastwood (1996), Finch (1981d), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Gilliard & LeCroy (1967b), Gregory (2000), Hartert *et al.* (1936), Hoogerwerf (1964), Iredale (1956), Knowles & Nitchen (1995), Mackay (1970), Mees (1982), Pearson (1975b), Rand (1938, 1942a), Rand & Gilliard (1967), Ripley (1964), Stattersfield & Capper (2000), Stein (1936), Weston (1975).

### 39. Rufous-lored Kingfisher

#### *Todiramphus winchelli*

**French:** Martin-chasseur de Winchell **German:** Rotnackeläst **Spanish:** Alción Cuellirrojo  
**Other common names:** Winchell's Kingfisher

**Taxonomy.** *Halecyon Winchelli* Sharpe, 1877, Isabella, Basilan. Genus often merged into *Halecyon*. Five subspecies recognized.

#### **Subspecies and Distribution.**

*T. w. nesydrionetes* (Parker, 1966) - C Philippines, on Tablas, Romblon and Sibuyan; probably this race on Masbate and Sicogon.

*T. w. nigrorum* (Hachisuka, 1934) - Samar, Calicoan, Biliran, Leyte, Negros, Cebu, Siquijor and Bohol.

*T. w. mindanensis* (Parker, 1966) - Mindanao.

*T. w. winchelli* (Sharpe, 1877) - Basilan.

*T. w. alfredi* (Oustalet, 1890) - Sulu Archipelago (Bongao, Sanga Sanga, Papahag, Tawitawi, Jolo).



**Descriptive notes.** 25 cm; male 60-64 g, female 67-80 g. Medium-sized kingfisher with dark blue upperparts, paler blue crown sides and rump, rufous supraloral spot. Male of nominate race has rufous hindcollar, white underparts; bill black; iris dark brown; legs and feet greyish-black, soles yellow. Female washed buffy-orange on underparts. Juvenile duller, black barring on rufous collar and breast. Races vary in hue of upperparts and colour of female's underparts: *nesydrionetes* female orange neck side and breastband; *nigrorum* distinctive bluish-black patch at side of breast; *mindanensis* blue areas strongly tinged purple, female

washed cinnamon below; *alfredi* male buff below. **Voice.** Rising series of 3-6 harsh metallic "chup"

notes, first 2 slower, rest faster, c. 1-5 seconds long, repeated every 3 or 4 seconds; also longer, faster series 6-8 seconds long, first 3 notes rising, followed by long, descending, decelerating series of up to 20 or more notes, repeated at intervals of c. 10 seconds.

**Habitat.** Dense lowland forest, preferably undisturbed, to 750 m, locally to 1000 m on Mindanao. **Food and Feeding.** Large insects, including grasshoppers (Orthoptera), cicadas (Cicadidae), beetles (Coleoptera), larvae; also spiders. Usually seen in higher parts of the canopy, but takes prey also from ground; large items are battered before being swallowed.

**Breeding.** Male with moderately large testes in May. No other information.

**Movements.** Presumably sedentary.

**Status and Conservation.** **VULNERABLE**. Population estimated at 2500-10,000 individuals, and declining rapidly. Recent records from c. 15 scattered localities, on Sibuyan, Masbate, Biliran, Cebu, Leyte, Bohol, Siquijor, E Mindanao, and 3 islands in Sulu Archipelago; present in areas afforded varying degrees of protection, including Mt Guitingitun on Sibuyan, Rajah Sikatuna National Park on Bohol, and the tiny Central Cebu National Park on Cebu. Rare at most known sites, where probably only relict populations; possibly extinct on Negros, and on some smaller islands. Reported as still locally common in Sulu Is in mid-1990's, and at Bislig (E Mindanao) in 1997, but both sites severely threatened: in Sulu Is, primary forest almost totally cleared and plans exist to replace few remaining areas of forest with oil palm (*Elaeis guineensis*) plantations; at Bislig, forest being cleared for commercial replanting with exotic trees. Illegal logging a major threat to key site of Rajah Sikatuna National Park. Main threat throughout range is extensive deforestation, particularly since this species seems to be a lowland specialist. Factors governing its distribution poorly understood; not known to what extent, if any, it may require fresh water: some evidence that it prefers forest on limestone, which would make it tolerant of open and more degraded forest, but it may simply prefer large trees, which now largely confined to uncultivable limestone areas. In addition, more information on its biology is urgently required.

**Bibliography.** Anon. (1997a), Brooks, Dutton, Gabutero & Timmings (1995), Brooks, Dutton, King & Magsalay (1996), Brooks, Evans *et al.* (1992), Brooks, Magsalay *et al.* (1995), Collar, Crosby & Stattersfield (1994), Collar, Mallari & Tabaranza (1999), Delacour & Mayr (1946), Dickinson *et al.* (1991), Dutton (1994), Dutton *et al.* (1996), Evans, Dutton & Brooks (1993), Evans, Magsalay *et al.* (1993), Hachisuka (1933), Hornskov (1996), Inskipp *et al.* (1996), Kennedy *et al.* (2000), McGregor (1909-1910), Parkes (1966), duPont (1971), duPont & Rabor (1973a), Potter (1953), Rand & Rabor (1960), Robson & Davidson (1996), Stattersfield & Capper (2000), Tomlinson (2000).

### 40. Blue-and-white Kingfisher

#### *Todiramphus diops*

**French:** Martin-chasseur des Moluques **German:** Lasurliäst **Spanish:** Alción Moluqueño  
**Other common names:** Moluccan/North Moluccan Kingfisher

**Taxonomy.** *Alcedo diops* Temminck, 1824, Amboina, Timor and Sulawesi; error = Ternate.

Genus often merged into *Halecyon*. Forms a superspecies with *T. lazuli*, *T. macleayii*, *T. albonotatus*, *T. leucopygius* and *T. farquhari*. Formerly considered conspecific with *T. lazuli*. Monotypic.

**Distribution.** N Moluccas, on Morotai, Halmahera, Ternate, Tidore, Moti, Bacan, Obilatu, Obi, Damar and Ngelele.



**Descriptive notes.** 19 cm; male 41-45 g, female 42-65 g. Male large white supraloral spot, dark blue head, wings and tail, pale blue back and rump; distinctive white patch at base of inner primaries in flight; white collar and underparts; bill black; iris dark brown; legs and feet blackish, soles yellow. Distinguished from larger *T. chloris* by much bigger white supraloral spot, white wing patch. Female lacks white collar, has broad blue breastband. Juvenile rufous loreal spot, collar and sides of breast and flanks. **Voice.** Warbling "tu-tu-tu-ti-ti", and fairly high-pitched, 3-note descending whistle, repeated continually.

**Habitat.** Secondary woodland and forest, and mangrove edges, also wooded gardens, lightly wooded cultivated land, orchards and coconut groves; sea-level to 700 m.

**Food and Feeding.** Only grasshoppers (Orthoptera) recorded. Perches in the open, often on dead tree or wire; at forest edges sits mainly in lower half of the trees.

**Breeding.** No information.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Restricted-range species; present in Northern Maluku EBA. Common over most of its range, although uncommon on Ternate. Seems to have adapted well to human disturbance and cultivation. More information is required on its biology and feeding ecology.

**Bibliography.** Andrew (1992), Coates & Bishop (1997), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Hartert (1903), Heinrich (1956), Inskipp *et al.* (1996), Knowles & Nitchen (1995), Lamberti (1994), Linsley (1995), Ripley (1959b), Stattersfield *et al.* (1998), Stresemann (1940), Sujatnika *et al.* (1995), Tomlinson (2000), White & Bruce (1986).

### 41. Lazuli Kingfisher

#### *Todiramphus lazuli*

**French:** Martin-chasseur lazuli **German:** Lazuliläst **Spanish:** Alción Lapizlázu  
**Other common names:** Lazuline/South Moluccan Kingfisher

**Taxonomy.** *Alcedo lazuli* Temminck, 1830, Sumatra; error = Ambon.

Genus often merged into *Halecyon*. Forms a superspecies with *T. diops*, *T. macleayii*, *T. albonotatus*, *T. leucopygius* and *T. farquhari*. Formerly considered conspecific with *T. diops*. Monotypic.

**Distribution.** S Moluccas, on Seram, Ambon and Haruku.

**Descriptive notes.** 22 cm. Male has white supraloral spot, dark blue crown, paler blue upperparts, darker blue ear-coverts, wings and tail; white throat, partial collar and breast, pale blue belly; bill mostly black; iris dark brown; legs and feet brown-black. Female breast and belly blue. Juvenile





buffy loreal spot and throat, black-speckled collar and breast. Voice. A series of rapid, short, high-pitched notes, "ke-ke-ke", lasting 6-20 seconds, during long bouts varies in speed before ending with harsh downslur, similar call starts with slower and more plaintive "ki-ki-ki..." series, increasing in tempo and becoming disyllabic "kee-kik", concluding with harsh trisyllabic notes, total length 12-26 seconds. **Habitat.** Lowland forest, forest edge, partly cleared forest, heavily degraded forest, secondary growth with cultivation, swampy woodland, and occasionally mangroves; from sea-level to 640 m.

**Food and Feeding.** Grasshoppers (Orthoptera) and beetles (including Cerambycidae). Watches for prey from a clear but shaded perch in middle to lower canopy, or from dead tree or wire in the open. **Breeding.** Little known: record of 4 recently fledged young being fed by both parents in early Dec. **Movements.** Presumed to be sedentary.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Previously considered Vulnerable. Restricted-range species: present in Seram EBA. Has a limited distribution and, although locally common in some areas, it is uncommon or absent in other areas of apparently suitable habitat. Despite habitat alteration, apparently not immediately at risk; appears able to thrive in heavily degraded coastal habitats; density of 4 birds/km<sup>2</sup> in logged and unlogged forest combined. Possibly requires dead forest trees for nesting, and these are usually removed from cultivated areas. More information on its biology is urgently needed.

**Bibliography.** Andrew (1992), Bishop (1992), Bowler (1993), Bowler & Taylor (1989), Coates & Bishop (1997), Collar *et al.* (1994), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Inskipp *et al.* (1996), Isherwood, Edwards *et al.* (1998), Isherwood, Willis *et al.* (1997), Knowles & Nitcher (1995), Mountfort (1988), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Stresemann (1914), Sujatnika *et al.* (1995), Tomlinson (2000), White & Bruce (1986).

## 42. Forest Kingfisher

### *Todiramphus macleayii*

**French:** Martin-chasseur forestier **German:** Spiegelliest **Spanish:** Alción de Macleay  
**Other common names:** Blue/Bush/Macleay's Kingfisher

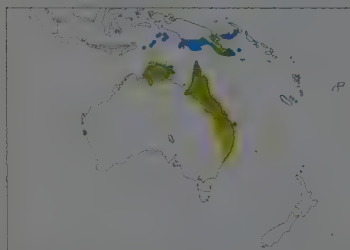
**Taxonomy.** *Halcyon Macleayii* Jardine and Selby, 1830, Port Essington, Northern Territory, Australia.

Genus often merged into *Halcyon*. Forms a superspecies with *T. diops*, *T. lazuli*, *T. albonotatus*, *T. leucopygius* and *T. farquhari*. Race *elizabeth* barely separable from nominate. Three subspecies tentatively recognized.

#### Subspecies and Distribution.

*T. m. elizabeth* (Heine, 1883) - E New Guinea, E from Astrolabe Bay in N and from Hall Sound in S. *T. m. macleayii* (Jardine & Selby, 1830) - N Australia in N Northern Territory (S at least to R Victoria), including Groote Eylandt and Sir Edward Pellew Group; some probably migrate to Sermata (E Lesser Sundas) and Aru Is.

*T. m. incinctus* (Gould, 1838) - Cape York Peninsula S to NE New South Wales (S to R Macleay); S population migrates N as far as SE Moluccas (Kai Is) and S New Guinea.



**Descriptive notes.** 20 cm; male 32-43 g, female 29-44 g. Smallish kingfisher with blue and white plumage. Male nominate race prominent white loreal spot, dark blue crown, black ear-coverts, white collar, paler blue upperwing-coverts and tail; prominent white wing spot in flight; white underparts; bill black above, lower mandible pinkish-brown basal half and blackish-brown distally; iris dark brown; legs and feet greyish-black. Female dark blue hindneck, buffy flanks. Juvenile buff loreal spot, breast and belly, blues duller, buff edges to crown and wing-coverts. Race *incinctus* greener back, scapulars and tertiaries,

smaller white wing spot; *elizabeth* darker blue upperparts. VOICE. "High Rolling Call" a repeated high-pitched "pee-pee-pee", by male in display; "Machine Gun Call" short bursts of rapidly repeated notes; also harsh, strident "scissor-wee-ya, scissor-wee-ya" chatter, soft repeated "seet" notes in flight, also short sharp click, and loud scream; "Attack Call" a short harsh "chtzaa"; "Grizzle" a soft, buzzing "grzzz"; young very vocal with begging call like the adult grizzle.

**Habitat.** Forest bordering swamps, monsoon forest, wet *Melaleuca* forest, mangroves, open eucalypt (*Eucalyptus*) forest, also forest edges and clearings, wooded swamps and creeks, screw-pine (*Pandanus*) savanna; also lightly wooded country including farmland, pasture, cropland, and suburban parks and gardens. Highest densities in N Australia in mixed riparian open forest, followed by tall closed swamp-forest, then tall dense grassland-forest. Migrants of race *incinctus* occupy humid habitats, forest clearings and edges in Papua New Guinea. In S Australia much more common below 200 m, but in N has wider altitudinal range, and up to 1700 m in Papua New Guinea.

**Food and Feeding.** Diet comprises wide range of invertebrates, including grasshoppers (Acrididae), stick-insects (Phasmida), cockroaches (Blattodea), beetles (*Chrysomelids*, *Heteromyzids*), ants (Formicidae), bugs (Hemiptera), cicadas (Cicadidae), adult and larval butterflies, dragonflies (*Aeshna*), spiders (*Lycosa*), worms (Lumbricidae); also small vertebrates, including fish (*Gambusia*), frogs and tadpoles, lizards (Scincidae, Agamidae), and snakes. Watches from perch on high bare branch or wire; plunges to the ground or water's edge to seize animal in bill (sally-pouncing), then returns to perch. Large items are beaten hard and repeatedly against perch, this often removing wings and elytra of insects, before being swallowed. Also takes prey from low vegetation, foliage, branches, tree trunks, and in air. In study in Kakadu National Park (Northern Territory), 56% of foraging was by sally-pounce, 43% by sally-strike (22% from foliage, 7% from ground, 5% from tree trunks, 8% from air), and 1% by plunging into water; 81% of dives were successful.

**Breeding.** Lays in Jan in Papua New Guinea, in Sept-Dec in Northern Territory, in Aug-Feb in Queensland, and in Oct-Dec in New South Wales: usually single-brooded in Northern Territory, but may rear 2 broods elsewhere. Often breeds as simple pair, but up to 3 helpers may assist. Territorial, migrants return to same territory in consecutive years. Male displays by sitting upright on a post, drooping wings, fanning and cocking tail, and calling vigorously, bill pointing skywards; male and female bow the head, spread wings, raise tail, and pirouette side by side on perch. Nest excavated by both adults, assisted by any helpers, usually in arboreal termitarium of *Nasutitermes*, sometimes in natural tree

hollow or in soil between roots of fallen tree, once excavated in a clump of staghorn ferns (*Polypodium*), and usually 4-12 m above ground, rarely more than 15 m; short inclined tunnel to nesting chamber, latter 23 cm in diameter. Clutch 3-6 eggs, usually 4 or 5; both parents incubate, possibly also helpers if present, incubation period c. 18 days, possibly 21 days; all also feed the young; a brood of 2 nestlings fed on 12-20 fish, frogs and lizards daily, but rejected insects; at one nest 3 helpers brought nearly 4 times as much food as the 2 parents; fledging period 27-31 days; adults feed fledglings for at least 1 month, then feeding rate declines, 75% of eggs hatched, and 50% of nestlings fledged; nests robbed by olive pythons (*Liasis olivaceus*) and goannas (*Varanus*); some young died in nest with injuries suggesting sibilicide, and nestlings sometimes harmed by infestations of scavenger moths.

**Movements.** Race *elizabeth* in Papua New Guinea resident; nominate race in Northern Territory also resident or partial migrant, and likely that some of that population move N to Sermata and Aru Is after breeding, although this needs confirmation. E Australian population *incinctus* is a partial breeding migrant S of Tropic of Capricorn, some birds arriving in S Queensland in Sept-Oct and leaving Mar-Apr, but some remaining all year; in N Queensland present all year, supplemented in autumn and spring by passage birds, and in winter may be more common in lowlands. Clear passage in Cape York Peninsula and islands in Torres Strait, but extent varies from year to year; non-breeding migrants found in S Moluccan archipelagos of Kai and Tanimbar, and from R Mimika in Irian Jaya through S Papua New Guinea to New Britain and, rarely, New Ireland and Solomon Is (Kolombangara); possibly migrates in family units, since groups of 6 seen in SE New Guinea. Possibly also some local seasonal movements; recorded as vagrant in E Victoria.

**Status and Conservation.** Not globally threatened. Widespread, and found in a range of habitats. Density of 0-4 birds/ha in Kakadu National Park; elsewhere in Northern Territory densities of 0-0.7-0.96 birds/ha, highest in mixed riparian open forest. In winter 1960, 1900 birds were counted along 160 km of road in N Queensland. Clearance of woodland for development has affected some populations, and a number of individuals are killed in collisions with windows and lighthouses.

**Bibliography.** Andrew, D. & Rogers (1993), Andrew, P. (1992), Anon. (1976), Barker & Vestsjens (1989), Beehler (1978), Beehler *et al.* (1986), Bell (1961, 1981, 1982a, 1986), Beruldsen (1990), Blakers *et al.* (1984), Bourchier (1978), Bravery (1970), Clancy (1982), Coates (1985), Coates & Bishop (1997), Crawford (1972), Deignan (1964), Diamond (1972), Doughty *et al.* (1999), Dow (1980), Eastman (1970), Finch (1982), Frith & Hitchcock (1974), Gilliard (1950b), Gosper & Gosper (1996), Gyldenstolpe (1955a), Hall (1974), Haselgrove (1975), Higgins (1999), Hindwood (1959), Inskipp *et al.* (1996), Keast (1961), Keast *et al.* (1985), Lindsey (1992), Longmore (1978), Macdonald (1988), Mackay (1977), Mayr & Rand (1937), Mees (1982), Peckover & Filwood (1976), Pizzey & Knight (1997), Rand & Gilliard (1967), Roberts, G.J. (1979), Roberts, N.L. (1941), Romer (1996), Rose (1997), Schodde & Hitchcock (1986), Schodde & Tidemann (1986), Simpson & Day (1998), Storr (1953, 1973, 1977), Strahan (1994), Taplin (1991), Thomson (1935), Tronson & Tronson (1987), Weston (1975), White & Bruce (1986), Woinarski, Press & Russell-Smith (1989), Woinarski, Tidemann & Kerin (1988).

## 43. New Britain Kingfisher

### *Todiramphus albonotatus*

**French:** Martin-chasseur à dos blanc **German:** Weißrückenliet **Spanish:** Alción Dorsiblanco  
**Other common names:** White-backed/White-mantled Kingfisher

**Taxonomy.** *Halcyon (Cyanalcyon) albonotata* E. P. Ramsay, 1885, New Britain.

Genus often merged into *Halcyon*. Forms a superspecies with *T. diops*, *T. lazuli*, *T. macleayii*, *T. leucopygius* and *T. farquhari*. Monotypic.

**Distribution.** New Britain (Bismarck Archipelago).



**Descriptive notes.** 16-18 cm; male 32 g. Male has white supraloral spot, light blue crown, black mask, dark blue wings and tail; remainder of body white; bill black, often horn-colored base of lower mandible; iris dark brown; legs and feet greyish-black. Female dark blue lower back and rump. Juvenile duller, white parts of plumage washed with buff, buff edges to upperwing-coverts. VOICE. Rapid series of 4 descending notes, "kee-ku-ko-ko", or light cackling trill, "ki-ki-ki-ki".

**Habitat.** Mainly lowland primary forest, but recorded also from secondary forest, disturbed and logged forest, forest edges and clearings;

sea-level to 1000 m.

**Food and Feeding.** Large insects, including crickets (Grylloidea) and grasshoppers (Orthoptera). Spends much time in upper canopy, but also perches lower down, scanning for prey on ground; swoops down to catch it and then returns to perch, where insects often beaten against branch before being swallowed.

**Breeding.** Lays in Aug-Oct. Pair-members sit near each other high in canopy, and call back and forth. Tunnel and nest-chamber dug by both adults in arboreal termitarium, 2 m above ground. Clutch 2-3 eggs; no information on incubation and nesting periods.

**Movements.** Apparently sedentary.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Restricted-range species: present in New Britain and New Ireland EBA. Despite being widespread in New Britain, it appears to be scarce, although easily overlooked in forest canopy unless calling. Is generally found only in primary and tall secondary forest to 1000 m, and this habitat is severely threatened by logging and clearance for oil palm (*Elaeis guineensis*) plantations. If this species proves to be intolerant of logged forest, its conservation status will need to be reclassified as Threatened. More information is required on its biology.

**Bibliography.** Coates (1985), Diamond & Marshall (1977), Dutson (2000), Eastwood (1995b), Fletcher (2000a), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Gilliard & LeCroy (1967a), Knowles & Nitcher (1995), Mountfort (1988), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Tomlinson (2000), Whentley (1998).

## 44. Ultramarine Kingfisher

### *Todiramphus leucopygius*

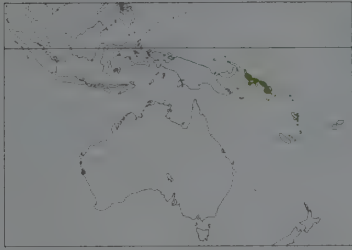
**French:** Martin-chasseur outremer **German:** Ultramarinliet **Spanish:** Alción Ultramar

**Taxonomy.** *Cyanalcyon leucopygius* J. Verreaux, 1858, Solomon Islands.

Genus often merged into *Halcyon*. Forms a superspecies with *T. diops*, *T. lazuli*, *T. macleayii*, *T. albonotatus* and *T. farquhari*. Monotypic.

**Distribution.** Solomon Is, from Buka and Bougainville through Shortlands, Choiseul, Santa Isabel and the Floridas to Guadalcanal.





**Descriptive notes.** 21 cm; male 35-52 g, female 44-61 g. Male dark blue head and upperparts, apart from white collar and back, lilac lower rump; white underparts, rufous undertail-coverts; bill black; iris dark brown; legs and feet black. Female like male, but back and lower mantle dark purple-blue, not white. Juvenile buffy underparts, blackish barring on breast and collar. **VOICE.** Quite vocal; rapid, high-pitched rattling "kidek-kidek-kidek" or "kakatakatakata"; other calls include descending "chew-cho-tew", and quiet nasal "keekow!".

**Habitat.** Dense primary and secondary lowland forest, *Casuarina* groves, forest margins, regenerating scrubland, wooded gardens and scattered trees; from sea-level to 2000 m. Uncommon within primary forest, more common in forest edge and secondary forest.

**Food and Feeding.** Insects and spiders recorded. Sits quietly in deep shade, or in the open, on trees and wires, watching for prey, which obtained mainly near the ground.

**Breeding.** Lays in Aug-Oct on Bougainville. Mutual bowing a probable courtship display. Nest dug into arboreal termitarium. No other information.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in Solomon Group EBA. Varies in abundance, from rare (e.g. on Choiseul) to fairly common (e.g. on Guadalcanal). On Guadalcanal occurs in parks and around fringes of capital town, Honiara. Tolerance of highly degraded habitats suggests that it is not under threat. More information is required on its biology.

**Bibliography.** Baker (1948), Cain & Galbraith (1956), Coates (1985), Diamond (1975), Donaghy (1950), Doughty *et al.* (1999), Dutson (2000), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Galbraith & Galbraith (1962), Hadden (1981), Henderson (1981), Kaestner (1987), Knowles & Ntchen (1995), Mayr (1945), Stattersfield *et al.* (1998), Webb (1992, 1997).

## 45. Chestnut-bellied Kingfisher

*Todiramphus farquhari*

**French:** Martin-chasseur à ventre roux **German:** Braunbauchliest **Spanish:** Alción Ventrirrufo

**Taxonomy.** *Halcyon farquhari* Sharpe, 1899, Malakula and Espiritu Santo, Vanuatu. Genus often merged into *Halcyon*. Forms a superspecies with *T. diops*, *T. lazuli*, *T. macleayii*, *T. albonotatus* and *T. leucopygius*. Monotypic.

**Distribution.** NC Vanuatu, on Espiritu Santo, Malo and Malakula.



**Descriptive notes.** 21 cm; male 32-42 g, female 35-42 g. Male has dark blue crown, white collar, dark blue back, wings and tail; white throat, distinctive orange breast, belly and undertail-coverts; upper mandible black, lower with pale horn base; iris dark brown; legs and feet greyish-black. Female has white patch on lower belly. Juvenile duller, white areas on head and neck washed with rufous. **VOICE.** High-pitched series of chirps repeated for over a minute, becoming faster as it rises in pitch; also a chirping note, and harsh "each-cach" as alarm.

**Habitat.** Mainly primary, undisturbed forest, usually in lowlands, locally in hills and lower mountains to at least 700 m; also occurs in gardens, farmland and coconut groves on Malo I. On Espiritu Santo and Malakula not found in the more open habitats, where it probably faces competition from *T. chloris*. Uses both the canopy and the understorey within the forest.

**Food and Feeding.** Insects, including beetles (Coleoptera), small grasshoppers (Orthoptera), ants (Formicidae), moths; also spiders, and lizards. Perches high in canopy, scanning for prey; prey

caught in flight, in foliage, on branches and tree trunks, or from the ground. Sometimes forages on ground, probing in litter or turning over soil for insects.

**Breeding.** Lays in Dec on Espiritu Santo. Nest excavated in arboreal termitarium or in hole in palm or tree fern. Clutch 3 eggs; no information on other aspects of breeding.

**Movements.** Presumably sedentary.

**Status and Conservation.** **VULNERABLE.** Restricted-range species: present in Vanuatu and Temotu EBA. Has very small range and specific habitat requirements for primary rainforest, which is severely threatened by logging. On Malo I, 8-10 pairs were found on a walk from the coast to the summit of Pic Malo, territories c. 200 m apart. Less common on Espiritu Santo, where it is excluded from open and most secondary habitats by *T. chloris*. Occurs in two protected areas on Espiritu Santo: is locally common at Loru, where estimated c. 100 birds/km<sup>2</sup>, but less common at Big Bay. As well as being threatened by logging, it may be adversely affected by habitat degradation caused by feral pigs and cattle. Additional information required on its breeding biology.

**Bibliography.** Bowen (1995, 1997), Bregulla (1992), Collar *et al.* (1994), Diamond & Marshall (1976, 1977), Doughty *et al.* (1999), Dutson (2000), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Knowles & Ntchen (1995), Medway & Marshall (1975), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Tomlinson (2000).

## 46. Sombre Kingfisher

*Todiramphus funebris*

**French:** Martin-chasseur funèbre **German:** Molukkenliest **Spanish:** Alción Sombrio  
**Other common names:** Funereal/Halmahera/Moluccan/Olive-backed Kingfisher

**Taxonomy.** *Todiramphus funebris* Bonaparte, 1850, Sulawesi; error = Moluccas.

Genus often merged into *Halcyon*. Monotypic.

**Distribution.** N Moluccas (Halmahera, Ternate).



**Descriptive notes.** 30 cm. Medium-sized kingfisher with stout bill. Male has white supraloral spot, supercilium and collar, dark olive-green or black upperparts, green-blue rump, white underparts; upper mandible black, lower mandible dark distally and on cutting edges with yellowish-horn base; iris dark brown; legs and feet black. Female duller and much browner. Juvenile even duller, lacking olive wash, has dark edges to white feathers of collar and breast, white-tipped bill. **VOICE.** Slow, distinctive "ki...ki...ki...ki"; also 3 loud, descending, maniacal-sounding notes for 1-5 seconds, repeated at 5-second intervals; another bird may reply with loud, repeated nasal disyllabic upslur at 1 per second.

**Habitat.** Swamp-forest (sago palm), tall secondary woodland, forest edge, mangroves, and occasionally gardens, cultivated lowlands and coconut plantations; coastal lowlands to 620 m, mostly below 100 m.

**Food and Feeding.** Large arthropods, including grasshoppers (Orthoptera) and centipedes (Chilopoda), also snakes. Perches for long periods on a shady branch in the middle level of trees, scanning clearings, before swooping to the ground for prey.

**Breeding.** No information available.

**Movements.** Probably sedentary.

**Status and Conservation.** **VULNERABLE.** Restricted-range species: present in Northern Maluku EBA. Uncommon, local and little known. Small population declining as a result of increasing loss and degradation of habitat. Destruction and fragmentation of forest has accelerated since early 1990's; commercial exploitation of valuable trees now widespread and heavy, and most of the remaining forest is now under timber concession. Habitat under further pressure from increased settlement and transmigration, with land-use changes such as conversion to agriculture, plantations, and irrigation schemes; also from mineral extraction and fuelwood-gathering. As this species seems clearly to prefer low elevations, such threats are especially worrying. More information on its biology is also needed.

**Bibliography.** Andrew (1992), van Bemmelen (1948), Coates & Bishop (1997), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Heinrich (1956), Inskipp *et al.* (1996), Knowles & Ntchen (1995), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Sujatnika *et al.* (1995), White & Bruce (1986).

inches 5  
cm 13





## 47. Collared Kingfisher

### *Todiramphus chloris*

**French:** Martin-chasseur à collier blanc **German:** Halsbandliest **Spanish:** Alción Acollarado  
**Other common names:** Black-masked/Mangrove(!)/White-collared Kingfisher; Sordid Kingfisher (*sordidus*)

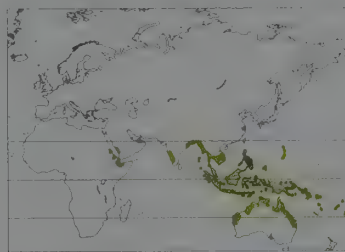
**Taxonomy.** *Alcedo Chloris* Boddaert, 1783, Cape of Good Hope; error = Buru. Genus often merged into *Halcyon*. Closely related to *T. enigma* and *T. cinnamominus*; former has been treated as conspecific, but lives alongside present species without hybridizing. Also close to *T. sanctus* and *T. tutus*, and some of the races listed below may be better placed in one of these, e.g. *regina*, *vitiensis* and *eximius* sometimes placed in former, whereas *marinus*, *sacer*, *manuae* and *pealei* may be better considered races of latter. Of numerous races named, some (e.g. *albicilla*) are distinctive but several others doubtfully valid; further research and revision desirable. Forty-nine subspecies currently recognized.

#### Subspecies and Distribution.

- T. c. abyssinicus* (Pelzeln, 1856) - S Red Sea coasts from NE Sudan to NW Somalia and in W Arabia.  
*T. c. kalbaensis* (Cowles, 1980) - S Arabian coast of United Arab Emirates (Khawr Kalba) and NW Oman (Shnass).  
*T. c. vidali* (Sharpe, 1892) - W India from Ratnagiri S to Kerala.  
*T. c. davisoni* (Sharpe, 1892) - Andaman Is and nearby Cocos Is.  
*T. c. occipitalis* Blyth, 1846 - Nicobar Is.  
*T. c. humii* (Sharpe, 1892) - coasts of West Bengal E to Myanmar (including Mergui Archipelago) and S to Peninsular Malaysia, Tioman I and NE Sumatra.  
*T. c. armstrongi* (Sharpe, 1892) - interior of Myanmar and Thailand, Indochina and E China (Shaweshaan Is, in Jiangsu).  
*T. c. laubmannianus* (Grote, 1933) - Sumatra (except NE coast) to Borneo, including Bangka, Belitung and other intervening islands.  
*T. c. chloropterus* (Oberholser, 1919) - islands off W coast of Sumatra (Simeulue S to Sipora).  
*T. c. azelus* (Oberholser, 1919) - Enggano I (off SW Sumatra).  
*T. c. palmeri* (Oberholser, 1919) - Java, Bali, Bawean and Kangean Is.  
*T. c. collaris* (Scopoli, 1786) - Philippines.  
*T. c. chloris* (Boddaert, 1783) - Talaud and Sangihe Is S through Sulawesi, Banggai and Sula Is to Lesser Sundas (from Lombok eastwards) and E to W Papuan Is and NW New Guinea (coasts of Vogelkop and Onin Peninsulas).  
*T. c. sordidus* (Gould, 1842) - Aru Is, and N & NE coasts of Australia.  
*T. c. pilbara* (Johnstone, 1933) - NW Australia from R De Grey W to Exmouth Gulf.  
*T. c. teraokai* (Nagamichi Kuroda, 1915) - Palau Is.  
*T. c. owstoni* (Rothschild, 1904) - N Northern Marianas (Asuncion, Agrihan, Pagan, Almagan).  
*T. c. albicilla* (Dumont, 1823) - S Northern Marianas (Saipan, Tinian).  
*T. c. orii* (Takatsukasa & Yamashina, 1931) - S Northern Marianas (Rota).  
*T. c. matthiae* (Heinroth, 1902) - St Matthias Is (NC Bismarck Archipelago).  
*T. c. nusae* (Heinroth, 1902) - New Hanover, New Ireland (except SW) and Feni Is.  
*T. c. novaehiberniae* (Hartert, 1925) - SW New Ireland.  
*T. c. bennetti* (Ripley, 1947) - Nissau I (E of New Ireland).  
*T. c. stresemanni* (Laubmann, 1923) - islands between mainland New Guinea and New Britain (Witu, Umboi, Sakar, Long and Tolokiwa).  
*T. c. tristrani* (E. L. Layard, 1880) - New Britain.  
*T. c. colonus* (Hartert, 1896) - Louisiade Archipelago.  
*T. c. alberti* (Rothschild & Hartert, 1905) - W & C Solomons, from Buka and Bougainville E to Florida Is and Guadalcanal.  
*T. c. pavuvu* (Mayr, 1935) - Pavuvu, in Russell Is (C Solomons).  
*T. c. mala* (Mayr, 1935) - Malaita (E Solomons).  
*T. c. solomonis* (E. P. Ramsay, 1882) - San Cristobal and adjacent islands (E Solomons).  
*T. c. sorororum* (I. C. J. Galbraith & E. H. Galbraith, 1962) - Malaupaina and Malaulalo (E Solomons).  
*T. c. amoenus* (Mayr, 1931) - Rennell and Bellona (E Solomons).  
*T. c. ornatus* (Mayr, 1931) - Nendo and Tinakula (NW Santa Cruz Is).  
*T. c. brachyurus* (Mayr, 1931) - Reef or Swallow Is (NC Santa Cruz Is).  
*T. c. vicina* (Mayr, 1931) - Duff Is (NE Santa Cruz Is).  
*T. c. utupuae* (Mayr, 1931) - Utupua I (C Santa Cruz Is).  
*T. c. melanodora* (Mayr, 1931) - Vanikoro I (S Santa Cruz Is).  
*T. c. torresianus* (Mayr, 1931) - Hiu and Loh in Torres Is (N Vanuatu).  
*T. c. santoensis* (Mayr, 1931) - Banks Is S to Espiritu Santo and Malo (NC Vanuatu).  
*T. c. juliae* (Heine, 1860) - Ambae and Maewo S to Efate (C Vanuatu).  
*T. c. erromangae* (Mayr, 1938) - Erromango and Aneityum (S Vanuatu).  
*T. c. tannensis* (Sharpe, 1892) - Tanna (S Vanuatu).  
*T. c. regina* (Mayr, 1941) - Futuna I, in C Polynesia.  
*T. c. pealei* (Finsch & Hartlaub, 1867) - Tutuila (American Samoa).  
*T. c. manuae* (Mayr, 1941) - Ofu, Olosega and Tau, in Manua Is (American Samoa).  
*T. c. vitiensis* (Peale, 1848) - Vanua Levu, Taveuni, Viti Levu, Koro, Ovalau and Ngau (Fiji).  
*T. c. marinus* (Mayr, 1941) - Lau Archipelago (E Fiji).  
*T. c. eximius* (Mayr, 1941) - Kadavu (S Fiji).  
*T. c. sacer* (J. F. Gmelin, 1788) - C & S Tonga.

Several other, apparently undescribed, populations in Santa Cruz Is (Tikopia, Anuta).

**Descriptive notes.** 23-25 cm; male 51-90 g, female 54-100 g. Medium-sized kingfisher with variable plumage pattern. Male nominate race white supraloral spot, black mask extending in narrow band across hindneck, white collar, greenish-blue crown and upperparts, brighter blue rump, blue wings and tail, white underparts; upper mandible grey-black, lower mandible yellowish-horn with dark brown cutting edges and tip; iris dark brown; legs and feet dark grey, soles yellowish. Female slightly duller. Juvenile duller, greener above and buffier below, neck and breast feathers fringed with dark grey, upperwing-coverts tipped with buff. The many races vary slightly in size but mainly in colour of plumage, upperparts being bluer or greener or more olive-toned than nominate, white loral spot of some extending variably as white or coloured supercilium, underparts varying from white to buff: *matthiae* crown varies from being dark green to being white with a few dark green feathers; *albicilla* distinctive with white head, narrow black eyeband, thin black nuchal line; *utupuae* and *juliae* rufous supercilium; *ornatus* and *tristrani* strongly buff below, latter with rufous loral spot; *vitiensis* supercilium rufous at front and buff at rear; several races, including previous and also



*alberti*, *orii*, *amoenus*, *brachyurus*, *vicina*, *santoensis* and *pealei*, show sexual dimorphism, with male generally buffier or more rufous underparts, forehead or supercilium. **VOICE.** Common call a loud, ringing or harsh "kee-kee-kee-kee", repeated 3-5 times, often when flying off, but some geographical variation: in Australia usually 2 (occasionally 3) notes as "kek kek", in Palau repeated "tchup-weee" in flight, and in Marianas "caw-heee" and loud barking "kip-kip-kiup"; in Samoa, last call higher-pitched and a drawn-out "kreecp" also uttered. Other calls: in Australia, strident, repeated rising "keer keer" trill by pair-members when near each other, a harsh metallic "aank-aank-aank", also a shriek in alarm; in Wallacea, loud shriek, "kick kyew, kick kyew..."; in Borneo and Vanuatu, several different calls identified include a piping "pippph" repeated up to 27 times from high perch as territorial song, a harsh "cack-cack-cack" alarm descending in tone and decelerating, "chirrup-chirrup" when bird alights next to another, and various other squeaking or quiet calls.

**Habitat.** In W areas (Sudan to India) confined to mangroves on the coast and in tidal creeks; in SE Asia, while using coastal mangroves and other coastal vegetation, it also inhabits nearby coconut plantations, suburban gardens and roadsides, and found in gardens 26 km from coast and along rivers up to 40 km upstream in Malaysia; in Indonesia and the Philippines uses mangroves and other coastal growth, but also a range of cultivated land e.g. gardens, rice fields, coconut and palm plantations, also marshes, dry grassland with scattered trees, cleared woodland and regrowth on farms and forest edge; in Australia largely confined to mangroves on inlets, estuaries and tidal flats, sometimes inland on mangrove-fringed rivers, and occasionally in nearby monsoon forest or woodland. On smaller Pacific islands its habitat choice is influenced by other kingfishers: when competitors present it tends to remain coastal, but in absence of competitors it moves inland to savanna, forested hills and closed forest. From sea-level to c. 1000 m, to 1500 m in Java and Sumatra.

**Food and Feeding.** Coastal populations feed mainly on crustaceans such as shrimps and crabs having carapace width of 1-2 cm, also small fish, including mudskippers (*Periophthalmus*). Those away from coast take wider range of prey, including insects such as cicadas (Cicadidae), beetles (Scarabaeidae, Tenebrionidae), carpenter-bees (Xylocopidae) and wasps, grasshoppers (Acrididae), stick-insects (Phasmida), butterflies and moths; also spiders, earthworms (Oligochaeta), snails (Gastropoda), land crabs, frogs, lizards (Agamidae, Gekkonidae, Scincidae), and snakes up to 11 cm long; less commonly, eggs and nestlings of small birds such as honeyeaters (*Lichmera*), and mice. In Vanuatu, skinks, locusts and small fish each comprised 28% of prey items, butterflies and other insects 15%, and crabs 2%. Perches for long periods, with little activity, 1-3 m up; swoops down to take prey from the ground, mud or shallow water and returns with it to perch, where prey is battered before being eaten. Also takes prey from ground without landing, and snatches insects in mid-air; also surface-plunges into shallow water, sometimes after brief hover. Most prey taken within 30 m of perch in Peninsular Malaysia. Sometimes takes scraps in fishing villages, and catches small fish escaping from nets pulled up onto the beach. Reported probing into mud for prey on exposed tidal flats. Has been seen following smooth-coated otters (*Lutrogale perspicillata*) to catch fish disturbed by the mammals.

**Breeding.** Lays in Apr-Jul in Ethiopia, in Jun in United Arab Emirates; in Mar-Aug but mainly Apr-May in NE India and Bangladesh, in Mar-May in Andaman Is, in Feb-Mar in Nicobar Is, in Apr in Myanmar, in Mar-Jul in Thailand, in Dec-Aug (Oct) in Peninsular Malaysia, in Mar-Nov in Sumatra and Java, and in May-Jun in Borneo and Philippines; in Jul-Aug in Marianas, in Oct-Mar in New Guinea, in Aug-Nov in Solomons, in Oct in Vanuatu, in Dec in Fiji, and in Sept-Feb in Australia; usually 2 broods reared in each season. Breeds as solitary pairs; single record of 5 birds combining to dig nest-hole in dead tree stump in Fiji, but no other indication of co-operative breeding. Territory defended all year. Mutual chases low over trees in courtship-flights, and male courtship-feeds female prior to mating; mates spread wings in greeting. Nest excavated in arboreal termitarium, in rotten tree trunk or stump, in earth bank, in soil around roots of upturned tree, or in base of bird's-nest fern (*Asplenium*), or a natural hole in tree or one made by woodpeckers (*Dinopium javanense*) is used; in Vanuatu 56% of nests were in arboreal termitaria, 26% in rotten trunks of tree ferns and 18% in sound trunks of other trees and palms, and in Australia 50% in tree hollows and 43% in termitaria; holes in trees average 3-5 m above ground (1.5-30 m), higher in termitaria (mean 5-7 m) than in tree hollows (mean 1-4 m); both birds fly at the site and strike it with the bill, later cling to rim while digging with bill and using feet to remove debris; nest-tunnel 5-7.5 cm in diameter, 15-90 cm long, nest-chamber 10-15 cm wide, 10 cm high; pair in Borneo started 8 nest-holes, completed 2 or 3, and reared 2 broods in quick succession from different holes; in Australia, holes have been used twice in a season and for several seasons. Clutch 2-5 eggs, usually 3 in Australia and Peninsular Malaysia, with exceptional record of 7; period from laying to fledging c. 44 days; both parents feed the young, which fledge after 29-30 days. At a nest-site in Australia, over 3 seasons, 70% of eggs produced fledged young. Longevity 6-11 years, on basis of ringing studies on the Selangor coast, in Peninsular Malaysia.

**Movements.** Resident and sedentary in most parts of range, with post-breeding dispersal reported in some areas. Record in coastal SE Somalia in 1997 considered more likely to have involved a migrant. Evidence that some populations have much longer movements, e.g. recoveries of ringed birds in Philippines were 150-300 km away from the original site. Seasonal changes in numbers in Peninsular Malaysia, Borneo and New Guinea suggest movements of several 100s of km; in Peninsular Malaysia some have been caught at Fraser's Hill while flying at night, and an individual reported from an oil rig 200 km E of the peninsula. In Australia, present throughout year in most localities and, despite earlier statements, no evidence of migratory movements; all 16 recoveries of birds ringed in Australia, New Guinea and SW Pacific have been within 10 km of ringing site, but occasional vagrants on Christmas I indicate some longer movements. Accidental in Japan, where 2 records in S Ryukyus.

**Status and Conservation.** Not globally threatened. Very widespread species which is common to abundant in some localities. Has colonized inland Malaysia in second half of 20th century. Densities vary locally and regionally; in Solomon Is occupied territories were only 250 m apart in the most densely colonized coastal areas with palms, trees and open spaces, but were much sparser in deep forest farther inland; much less common along Australian coastline, with occupied territories varying from 1-5 ha to 10 ha near Brisbane on E coast, and even in N Australia, where considered common, this species is far less plentiful than *T. sanctus* in coastal habitat. Destruction of mangroves for coastal development could be a threat to some populations. Some subspecies on small Pacific islands, such as *vicina* and *brachyurus*, and possibly also *regina*,

have extremely small populations, and could be threatened by loss of habitat exacerbated by adverse effects of natural events.

**Bibliography.** Abdulali (1971), Ali (1996), Ali & Ripley (1983), Andrew & Rogers (1993), Anon. (1931), Archer & Goodman (1937-1961), Ash & Miskell (1998), Ashmole (1963), Aspinall (1996), Baker, E.C.S. (1934b), Baker, R.H. (1951), Banks (1984), Beaman (1994), Beckon (1987), Beehler *et al.* (1986), Berwick (1952), Bielewicz & Bielewicz (1996), Blakers *et al.* (1984), Bradley & Wolff (1956), Bregulla (1992), Brown (1984), Bucknill & Chasen (1990), Burton (1978b), Cain & Galbraith (1956), Clancey (1992), Coates (1985), Coates & Bishop (1997), Cowles (1980), Crawford (1972), Daniels (1997), Danielsen *et al.* (1994), Dasgupta & Basuroy (1989), Dhondt (1976a), Diamond (1975), Dickinson *et al.* (1991), Donaghy (1950), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Draffan *et al.* (1983), Edgar (1954), Edge (1990), Engbring & Ramsey (1989), Étchéopar & Hüc (1978), Evans, M.I. (1994), Ewart (1973), Fancy *et al.* (1999), Forshaw & Muller (1978), Fry (1980a), Fry *et al.* (1988), Gibson-Hill (1948), Gill (1970), Gilliard & LeCroy (1967a), Grimmett *et al.* (1998), Hall (1974), Harvey (1990), Hellebrekers & Hoogerwerf (1967), Higgins (1999), Hollom *et al.* (1988), Holmes & Wood (1980), Holyoak (1979), Hoogerwerf (1967, 1970), Isherwood *et al.* (1997), Jennings (1995), Jeyarajasingam & Pearson (1999), Johnstone (1983, 1990), Johnstone & Storr (1998), Kennedy *et al.* (2000), Law (1934), Lekagul & Round (1991), MacKinnon & Philipps (1993, 2000), Mackworth-Præd & Grant (1957), Madoc (1976), van Marle & Voous (1988), Mayr (1931, 1941, 1950), Mayr & Rand (1937), McClure (1998), Medway & Wells (1976), Mees (1986), Mitra (1980), Oberholser (1919), Pfeffer (1958, 1963), Phillips (1972), duPont (1976b), duPont & Rabor (1973a, 1973b), Porter *et al.* (1996), Rabor (1977), Rand & Gilliard (1967), Riley (1997a), Rinke (1988), Robson (2000a), Seitre & Seitre (1991), Sibley (1951), Smythies (1968, 1999), Snow (1978), Stagg (1984, 1985), Strahan (1994), Thompson (1984), Tikader (1984), Vince (1998), Vowles & Vowles (1984), Watling (1982), Webb (1997), Wells (1999), White & Bruce (1986), Zhao Zhengjie (1995).

## 48. Talaud Kingfisher

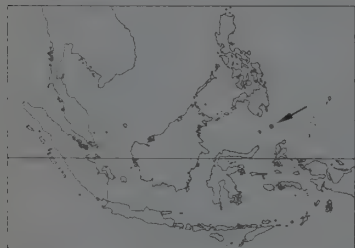
### *Todiramphus enigma*

**French:** Martin-chasseur des Talaud    **German:** Talautliet    **Spanish:** Alción de las Talaud  
**Other common names:** Obscure Kingfisher

**Taxonomy.** *Halcyon enigma* Hartert, 1904, Salebabu, Talaud Islands.

Genus often merged into *Halcyon*. Closely related to *T. chloris* and previously considered conspecific, but the two occur together without interbreeding. Also close to *T. cinnamominus*. Monotypic.

**Distribution.** Talaud Is (Kaburuang, Karakelong, Salibabu).



**Descriptive notes.** 21 cm. Both sexes have white loreal spot which extends to the eye, black mask, green crown and back with blue tinge on crown, green-blue wings and tail, white collar and underparts; bill black, lower mandible yellowish-horn with black cutting edges and tip; iris dark brown; legs and feet black. Distinguished from very similar *T. chloris* by smaller size, shorter bill and tail, and hunched posture giving dumpy appearance, also stronger green tinge above. Juvenile apparently undescribed. **Voice.** A 5-note "kee kee kee kee kee", notes equal in length and pitch, can be repeated 4-6 times; also "ki-kac" or "ki-kee".

second note drawn out and slightly descending, and "ki ki ki ki ki ki" alarm lasting 5-10 seconds.

**Habitat.** Forest and forest edge, preferring undisturbed areas, but also found in secondary forest; often feeds along rivers and streams, as well as in forest. Replaced in more coastal habitats and cultivated areas by *T. chloris*.

**Food and Feeding.** Small grasshoppers (Orthoptera) and river snails (Gastropoda). Usually perches in mid-canopy, 6-15 m up, scanning ground below; dives down on to prey.

**Breeding.** Pairs defending territories and probable courtship feeding reported in Sept and Oct. No other information.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Restricted-range species: present in Sangihe and Talaud EBA. Common, and apparently able to withstand some habitat disturbance, but has very restricted distribution. Occurs in Karakelong Hunting Reserve, and both there and in some other areas of forest on that island pressure exists from logging and deforestation; continuing habitat loss could lead to problems for this species. More information on its biology and status is urgently required.

**Bibliography.** Andrew (1992), Coates & Bishop (1997), Eek (1978), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Greenway (1978), Inskipp *et al.* (1996), Knowles & Nitchen (1995), Oberholser (1919), van Oosten &

Riley (1996), Riley (1997a, 1997b, 1997c, 1997d), Riley *et al.* (1998), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Sujatnika *et al.* (1995), White & Bruce (1986).

## 49. Micronesian Kingfisher

### *Todiramphus cinnamominus*

**French:** Martin-chasseur cannelle    **German:** Zimtkopfliegt    **Spanish:** Alción Micronesio  
**Other common names:** Caroline Islands Kingfisher (*reichenbachii*); Guam Kingfisher (*cinnamominus*); Ryukyu/Ryuki Kingfisher (*miyakoensis*)

**Taxonomy.** *Halcyon cinnamomina* Swainson, 1821, Northern Mariana Islands.

Genus often merged into *Halcyon*. Closely related to *T. chloris* and *T. enigma*. Extinct race *miyakoensis* of Miyako-jima (S Ryukyu Is) sometimes considered a full species, but information on bill colour lacking; probably better treated tentatively as race of present species. Three extant subspecies recognized.

**Subspecies and Distribution.**

*T. c. cinnamominus* (Swainson, 1821) - Guam (S Northern Marianas).

*T. c. pelewensis* (Wiglesworth, 1891) - Palau Is.

*T. c. reichenbachii* Hartlaub, 1852 - Pohnpei (E Caroline Is).



**Descriptive notes.** 20 cm; male 56-62 g, female 58-74 g. Distinctive small kingfisher. Male nominate race rufous head and underparts, black eyestripe, blue-green back, rump, wings and tail; bill dark apart from horn-coloured base of lower mandible; iris dark brown; legs and feet black. Female white lower breast and belly. Juvenile pale rufous throat, dusky markings on breast, buff belly. Race *pelewensis* both sexes rufous crown, black mask extending as thin line across nape, white neck and underparts; *reichenbachii* similar but larger, crown paler; extinct *miyakoensis* was like nominate, but no black line across nape, and

red legs and feet. **Voice.** On Guam, harsh "kskh-skshh-skshh-kroo-ee, kroo-ee, kroo-ee" and plaintive "kiu-kiu-kiu"; on Pohnpei, harsh "tchip-weer" and loud "kewp-kewp-kewp-kewp"; quieter on Palau, but chattering "che-che-che, che-kreek, kreek, kreek".

**Habitat.** Forest, woodland, mangrove swamps, coconut palms, and large gardens. Replaced by *T. chloris* in coastal habitats on Palau.

**Food and Feeding.** Insects, including grasshoppers (Orthoptera) and cicadas (Cicadidae), also skinks (Scincidae) and geckos (Gekkonidae). Perches on a low exposed branch, wire or forest vine, looking out for prey, which it usually takes on the ground.

**Breeding.** Lays in Dec-Jul on Guam and in Aug on Pohnpei. Both sexes excavate a hole 3-8 m above ground in a tall tree or coconut palm; natural hollow sometimes used; pair may control several nest hollows, but only one is used. Clutch 2 eggs; both parents feed the chicks; no information on incubation and fledging periods.

**Movements.** Probably sedentary.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in Nansei Shoto EBA (extinct), Mariana Islands EBA (extinct in wild), Palau EBA and East Caroline Islands EBA. Race *miyakoensis* is known only from a single specimen taken in 1887, subsequent to which the taxon was considered extinct; rumored to have been rediscovered in 1960's but without foundation; more recent ideas suggest it may have been a vagrant of this species from other parts of its range, a bird brought in as a pet, or possibly even a mislabelled specimen; DNA comparison with other races might help to clarify the situation. Population of nominate race on Guam extinct in wild since 1986, primarily as a consequence of the introduction of brown tree-snakes (*Boiga irregularis*); before extinction, 29 birds were captured for captive breeding; about 65 now in captivity in zoos in USA, and some may be reintroduced onto Guam in snake-controlled areas. Population on Pohnpei has declined, but species is not yet endangered there. Race *pelewensis* remains fairly common on the larger islands of Palau.

**Bibliography.** Anon. (1997b), Bahner (1993, 1994, 1995), Baker (1951), Baltz (1998), Beaman (1994), Beck & Savidge (1990), Bjorkmand & Seibels (1996), Brazil (1991), Buden (2000), Engbring (1988), Fuller (1987), Greenway (1967), Griffin *et al.* (1988), Haig & Ballou (1995), Haig *et al.* (1995), Hay (1986), Inskipp *et al.* (1996), Jenkins (1983), King (1978/79), Knox & Walters (1994), Marshall, J.T.J. (1949), Marshall, S.D. (1989), Oehler (1990), Pratt, Bruner & Berrett (1979, 1987), Pratt, Engbring *et al.* (1980), Shelton (1986, 1987, 1988), Sheppard (1986), Stophlet (1946), Takara & Kuroda (1969).





50

*ssp saurophagus*

*ssp admiralitatis*  
different crown patterns

*ssp recurvirostris*

51

*ssp sanctus*

*ssp interpositus*

*ssp dammerianus*

52

*ssp australasia*

*ssp mauke*

*ssp ruficollaris*

53

*ssp tutus*

*ssp veneratus*  
♂ ♀

*ssp atiu*

54

*ssp youngi*  
♂

55

56

57

*ssp flavivirostris*  
♂

*ssp sellamontis*  
♂

59

*ssp megarhyncha*  
♀

*ssp tarotoro*  
♀

58

*ssp ochracea*  
♂

*ssp wellsi*

PLATE 16

inches 4  
cm 10



## 50. Beach Kingfisher

### *Todiramphus saurophagus*

**French:** Martin-chasseur à tête blanche **German:** Echsenliest **Spanish:** Alción Lagartijero  
**Other common names:** White-headed Kingfisher

**Taxonomy.** *Halcyon saurophaga* Gould, 1843, between Yapen and Cape d'Urville, New Guinea. Genus often merged into *Halcyon*. Closely related to *T. chloris* but much larger. Race *anachoreta* merged with *admiralitatis* by some authors; at other extreme, population of Anchorite Is may warrant recognition as a separate race. Three subspecies currently recognized.

#### **Subspecies and Distribution.**

*T. s. saurophagus* (Gould, 1843) - N Moluccas, W Papuan Is, NW, N & SE coasts of New Guinea, New Britain, New Ireland and satellite islands, and Solomon Is (Bougainville to San Cristobal).

*T. s. anachoreta* (Reichenow, 1898) - Ninigo, Anchorite and Hermit Is (NW Bismarck Archipelago).

*T. s. admiralitatis* (Sharpe, 1892) - Admiralty Is (NW Bismarck Archipelago).



**Descriptive notes.** 30 cm; male 90-146 g, female 110-146 g. Large kingfisher. Both sexes nominate race white head, neck and underparts, small black line behind eye, green-blue back, wings and tail; bill dark apart from pale base of lower mandible; iris very dark brown; legs and feet black. Juvenile duller blues, buffy crown and underparts, breast feathers fringed with grey. Races differ mainly in crown pattern: *admiralitatis* usually broader eyeband, crown variable from blue-green in some to white in 60% of population, with intermediates; *anachoreta* crown white in half of population, green-blue in other half, but entire

population on Anchorite has blue-green crown. **Voice.** Similar to *T. chloris* but louder and deeper. "kill kill", or "kee-kee-kee" or "kio-kio-kio-kio"; also churring call when alighting in tree; "tink, tink" calls during courtship chases.

**Habitat.** Beaches with driftwood and a few perches, rocky shores, coral cliffs and pools, headlands, mangrove swamps, shores with overhanging trees and plentiful vegetation, also coconut plantations; occasionally visits garden ponds. From offshore islets to several hundred m inland. Generally rare or absent where *T. chloris* occurs.

**Food and Feeding.** Crabs, fish, insects and their larvae, and lizards. At low tide feeds mainly on crabs; at high tide moves into coastal vegetation, taking lizards and insects in and below the trees. Perches on a branch or exposed rock, post or driftwood, swooping down to the ground or shallows for prey. Sometimes hovers briefly before diving for fish; will forage up to 100 m offshore.

**Breeding.** Lays in Aug-Dec in New Guinea. Nest in tree hole or in end of hollow branch 3-5 m above ground, possibly sometimes in the fibrous tissue at top of coconut palm. Probable courtship display of high chases, with slow wingbeats and "tink" calls. Clutch 2-4 eggs; no information on incubation and fledging periods.

**Movements.** In dry season, May-Nov, some movements reported from offshore islands to mainland of N Papua New Guinea, near Madang.

**Status and Conservation.** Not globally threatened. Widespread, but little information on population levels; scarce in some areas and common in others. Recorded densities of up to 1-5 pairs/ha, and 8 pairs along 2 km of shoreline. Additional information required on its breeding biology.

**Bibliography.** Andrew (1992), Bailey (1992), Beehler *et al.* (1986), Bell (1970c, 1970d, 1975a), Blaber (1990), Bowler & Taylor (1989), Cain & Galbraith (1956), Coates (1985), Coates & Bishop (1997), Coates & Swainson (1978), Doughty *et al.* (1999), Eastwood & Hicks (1998), Giliard & LeCroy (1967a), Gregory-Smith & Gregory-Smith (1989), Gyldenstolpe (1955b), Hadden (1981), Harding (1982), Hartert (1903), Howell (1981), Hulme (1976), Inskipp *et al.* (1996), Lambert & Yong (1989), Mackay (1970), Mayr (1945), Mayr & Meyer de Schauensee (1939), Mees (1965), Rand & Giliard (1967), Ripley (1964), Schönwetter (1966), Sibley (1951), Tomlinson (2000), Webb (1992, 1997), Weston (1975), White & Bruce (1986).

## 51. Sacred Kingfisher

### *Todiramphus sanctus*

**French:** Martin-chasseur sacré **German:** Götzenliest **Spanish:** Alción Sagrado  
**Other common names:** Green/Tree/Wood Kingfisher; New Zealand Kingfisher (*vagans*); Flat-billed Kingfisher (*recurvirostris*)

**Taxonomy.** *Halcyon sanctus* Vigors and Horsfield, 1827, New South Wales.

Genus often merged into *Halcyon*. Forms a superspecies with *T. australasia*, *T. tutus*, *T. veneratus*, *T. gambieri* and *T. godeffroyi*; has been considered conspecific with *T. australasia*. Race *recurvirostris* sometimes considered a full species, but its characteristic flattened bill seems to represent the extreme of a trend seen in *maemillani*; subspecific treatment thus appears more appropriate. Races *regina*, *vitiensis* and *eximius* of *T. chloris* sometimes considered to belong in present species. Race *ruficollaris* of *T. tutus* possibly better included within present species. In past, race *ruficollaris* of *Alcedo azurea* inexplicably and erroneously listed under present species. Populations of Lord Howe I and Norfolk I sometimes separated as races *adamsi* and *norfolkensis* respectively, but they differ little from New Zealand *vagans*. Five subspecies currently recognized.

#### **Subspecies and Distribution.**

*T. s. sanctus* (Vigors & Horsfield, 1827) - Australia, and possibly also E Solomons (Guadalcanal, San Cristobal); migrates to Indonesia and Melanesia.

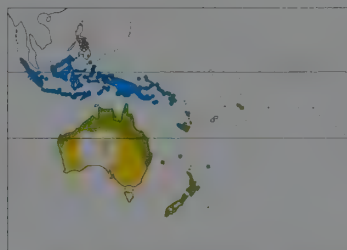
*T. s. vagans* (Lesson, 1830) - Lord Howe I, Norfolk I, Kermadec Is and New Zealand.

*T. s. canacorum* (Brasil, 1916) - New Caledonia and I of Pines.

*T. s. maemillani* (Mayr, 1940) - Loyalty Is.

*T. s. recurvirostris* Lafresnaye, 1842 - Apolima, Upolu and Savaii (Western Samoa).

**Descriptive notes.** 22 cm; male 28-61 g, female 28-56 g. Male nominate race buff loreal spot, dark green forehead and crown, black mask extending narrowly across nape at rear; upperparts green



to dark green, rump bright blue, upperwing-coverts blue-green, flight-feathers black with blue outer webs, tail blue with purple in centre and green at sides; throat white, collar light buff, breast buff, colour becoming more pronounced on flanks, belly and undertail-coverts; upper mandible blackish, lower pale horn with blackish tip and cutting edges; iris very dark brown; legs and feet black to dark pinkish-brown. Distinguished from *T. chloris* by smaller size, buff underparts. Female duller, greener, especially on wings and rump. Juvenile duller, buff edges to upperwing-coverts, dusky tips to feathers on cheeks, collar, breast

and flanks. Race *vagans* larger and duller, underparts more yellowish buff, *canacorum* smaller; *maemillani* underparts deeper buff or cinnamon, bill slightly flattened and shorter (38-5 mm); *recurvirostris* smaller than previous, deeper cinnamon on flanks, bill shorter (36 mm) and even more flattened dorsoventrally. **Voice.** "Staccato Call" a series of 4-5 (occasionally up to 12) repeated notes, "kik-kik-kik-kik-kik", mainly by male, used in territorial advertisement and courtship; "tucree-tucree-tucree" by both sexes as a greeting; shrill descending scream mainly by female to attract attention; harsh "kicha" when attacking a predator or intruder; harsh scream when caught by cat or by people; a range of other quiet calls known, some given mainly at night or from inside a nestbox.

**Habitat.** Typically, in Australia, breeds in eucalypt (*Eucalyptus*) woodland and open forest with sparse understorey and with over 50 mm of summer rainfall; also in *Acacia* scrub, tussock grassland with some taller trees, *Melaleuca* swamps, mangroves, depauperate rainforest, edges of monsoon rainforest, and along seashores, vegetated coastal dunes, sandy and coral cays and reefs; in Northern Territory, highest density (0-20 birds/ha) in tall closed *Melaleuca* swamp-forest, lower density (0-08 birds/ha) in low mangrove forest, and closed vine-thicket; occurs in open farmland, remnant roadside vegetation, parks and suburban gardens. In non-breeding quarters favours open parkland, trees with short grass and low cover, wooded roadside and forest edges, gardens, swamps and savannas; in Northern Territory moves to wetter habitats in the non-breeding (dry) season. In New Zealand found in many native forests, especially at edges or clearings; after breeding, moves to more open areas, farmland, and the coast, estuaries, lagoons and harbours with mudflats or rock platforms, and avoiding areas with increased ground cover of woody vegetation.

**Food and Feeding.** Wide variety of invertebrates, particularly insects, including locusts and grasshoppers (Acrididae), Gryllidae, Gryllotalpidae, Stenopelmidae, Tettigoniidae), dragonflies (Aeshnidae, Corduliidae, Zygoptera), flies (Calliphoridae, Tabanidae, Tachinidae), cockroaches (Blattellidae), various beetles (Carabidae, Cerambycidae, Chrysomelidae, Curculionidae, Elateridae, Geotrupidae, Hydrophilidae, Lucanidae, Scarabaeidae, Tenebrionidae), earwigs (Dermaptera), cicadas (Cicadidae), bugs (Pentatomidae), ants (Formicidae), bees and wasps (Apidae, Ichneumonidae, Pompilidae), moths and caterpillars (Hepialidae, Noctuidae), mantids (Mantidae), phasmids (Phasmidae); also spiders (Agelenidae, Araneidae, Dipluridae, Idiopidae, Lycosidae, Pisauridae), centipedes (Chilopoda), crustaceans (Cambaridae, Grapsidae, Parastacidae), worms (Lumbricidae), molluscs (Helicidae). Also small vertebrates such as fish (Cyprinidae, Poeciliidae, Salmonidae), tadpoles and frogs, lizards (Agamidae, Gekkonidae, Scincidae), snakes, small birds (*Acanthisitta*, *Carduelis*, *Gerygone*, *Passer*, *Zosterops*), and mice. Sits on vantage point, surveying area below for prey, occasionally bobbing head or flicking tail; swoops down to take food from the ground, briefly landing (sally-pounce), and returning with it to perch, where it is beaten and then swallowed. Prey also taken without landing (sally-strike), sometimes in a brief hover, from foliage, from the surface of mudflats, or in the air; takes prey from the surface of water without submerging, or sometimes shallowly submerging. In Kakadu National Park (Northern Territory), 44% of foraging attacks were sally-pounces, and 40% were sally-strikes in foliage, 8% on tree trunks, 8% in air, and less than 1% dives into water. Success rate in Kakadu was 86%; in New Zealand it was 96-6% for catching crabs on mudflats.

**Breeding.** Lays in Sept-Mar in Australia, but mainly Oct-Jan in S and similar in N; in Oct-Jan but mainly Nov-Dec in New Zealand; in Dec in New Caledonia and in Oct-Dec on Norfolk I, often 2 broods reared in succession; in SW New South Wales, many pairs bred during a flood year but none during drought years. Monogamous, in solitary pairs; pairs call and aggressively chase others from the territory. Most Australian nests in hole in tree, especially eucalypt (50%), also in arboreal termitarium of *Nasutitermes* (26%), in cliff or bank (5%), or in unspecified site in tree (19%), and tree hollow usually excavated by the birds but sometimes natural; other sites include road cuttings, old mine workings, mud walls, palm trees, tree ferns and epiphytic ferns; choice of site may depend on availability, with some regional preferences, e.g. for tree hollows in Western Australia, for arboreal termitaria in C New South Wales and for dead trees in New Zealand (North Island); mean height above ground 7 m for nests in eucalypts and arboreal termitaria; both sexes excavate, taking 2 days to 2 weeks, often several holes excavated before one chosen; tunnel c. 5 cm wide, c. 30 cm long in banks but as short as 7 cm in termitaria, often inclining slightly upwards before ending in chamber 12-20 cm in diameter; may return to nest-site in successive years; nest-sites used continuously for 21 years in S Queensland and 17 years in New Zealand. Clutch 3-7 eggs, usually 4 or 5, laying interval 2 days for first 2 or 3 eggs, then 1 day, or laid on successive days or irregularly; incubation by both sexes, period 16-18 days, in New Zealand 20-21 days; hatching nearly synchronous; both parents feed young about equally, but probably both do not brood; in New Zealand, young fed every 20 minutes in first week, then every 10 minutes; nestling period 24-29 days; parents feed young for 7-10 days after fledging, and fledglings from first brood may be chased from territory after 1-2 weeks. Hatching success 77-85%, fledging success 68%; overall success in Kakadu National Park 64%. Oldest ringed bird was 8 years.

**Movements.** Nominate *sanctus* in S Australia mostly migrates N after breeding, although a few remain behind, particularly on coast; migrates to New Guinea and Indonesia, moving W to Sumatra, N to Borneo and Talaud Is, and E to Solomon Is; nocturnal movement, leaving Australia on a broad front from the Arufura Sea to the Coral Sea, large numbers crossing the Torres Strait and exhausted birds arriving on islets off Port Moresby; juveniles may migrate N before adults; 2 ringed Australian birds recovered over 2500 km to N, but others probably travel 4000 km; ringing studies have shown that individuals return to same breeding and non-breeding sites in successive years. Present throughout year in N Australia, with numbers in Darwin peaking in Apr-May and Aug-Sept; more common along coast in winter. In New Zealand, race *vagans* shows altitudinal

On following pages: 52. Cinnamon-banded Kingfisher (*Todiramphus australasia*); 53. Chattering Kingfisher (*Todiramphus tuta*); 54. Tahiti Kingfisher (*Todiramphus veneratus*); 55. Tuamotu Kingfisher (*Todiramphus gambieri*); 56. Marquesas Kingfisher (*Todiramphus godeffroyi*); 57. Red-backed Kingfisher (*Todiramphus pyrrhopygius*); 58. Yellow-billed Kingfisher (*Syma torotoro*); 59. Mountain Kingfisher (*Syma megarhyncha*).



migration, with post-breeding movement from higher altitudes to the coast and also from forest to coast and open lands. Populations on Lord Howe I, Norfolk I and Kermadec Is are sedentary.

**Status and Conservation.** Not globally threatened. Widespread and common in many areas. Densities from various localities in Australia and New Zealand vary, 5–80 birds/km<sup>2</sup>, with an average of c. 20 birds/km<sup>2</sup>; some much higher estimates of density from New Guinea non-breeding quarters, where 90 birds in a 4-ha airstrip and 10 pairs along 600 m of road; very common in New Caledonia and Loyalty Is. Total Australian population estimated to be c. 60,000,000 birds. This species' range may be expanding into parts of C Australia, and numbers have possibly increased in New Zealand in 20th century. In some areas, forest clearance has provided open habitats suitable for its survival in non-breeding season, and roads with cuttings have provided additional nest-sites, but clearance has also removed tree holes: this kingfisher possibly did not colonize Norfolk I until land clearance by early settlers provided suitable habitat. Faces some competition from introduced species; pairs sometimes evicted from nesting hollows by Common Starlings (*Sturnus vulgaris*), Common Mynas (*Acridotheres tristis*) and sparrows (*Passer*). In addition, numbers are killed by cats, foxes (*Vulpes*) and stoats (*Mustela*), and by colliding with windows, powerlines, lighthouses and vehicles. Sometimes shot by humans for its attacks on bees, fish, poultry or cagebirds, or belief that it damages fruit in orchards.

**Bibliography.** Acres (1960), Andrew, D. & Rogers (1993), Andrew, P. (1992), Armstrong (1932), Ashmole (1963), van Balen & Johnstone (1997), Barker & Vestjens (1989), Barré & Dutton (2000), Bechler (1978), Bechler *et al.* (1986), Bell (1982a, 1986), van Bennekom (1975), Bismark & Somadikarta (1992), Blakers *et al.* (1984), Brooker (1987), Cain & Galbraith (1956), Chambers (1989), Child (1984), Coates (1985), Coates & Bishop (1997), Dhondt (1976b), Diamond (1972), Disney & Smithers (1972), Doughty *et al.* (1999), Draffan *et al.* (1983), Eastman (1970), Falla *et al.* (1981), Fitzgerald *et al.* (1986), Florey (1960), Forshaw & Muller (1978), Fraser & Henson (1996), Friih & Hitchcock (1974), Gosper (1983), Gosper & Gosper (1996), Goudswaard (1990), Grant (1983), Green & McGarvie (1971), Greenway (1966), Hall (1974), Hayes (1989, 1991), Heather & Robertson (1997), Hermes (1985), Hicks (1992), Higgins (1999), Hindwood (1940), Hobbs (1961), Holmes, D.A. & Philipps (1996), Holmes, P. & Wood (1980), Hoogerwerf (1948b, 1967), Horton (1975), Inskipp *et al.* (1996), Isherwood *et al.* (1997), Johnstone & Storr (1998), Keast (1957, 1993), Kinsky (1970), Lauret (1990), Lawson (1996), Lindsey (1992), Macdonald (1988), MacKinnon & Philipps (1993), van Marle & Voous (1988), Mason (1989), Mayr & Rand (1937), Mees (1949, 1965, 1982, 1986), Milhinch (1980), Moon (1991, 1992), Mordue (1981), O'Donnell (1981), Onley (1980), Pfeffer (1958), Pizzey & Knight (1997), duPont (1976b), Pratt *et al.* (1987), Ralph & Ralph (1977), Rand & Gilliard (1967), Reed (1980), Robertson, C.J.R. (1985), Robertson, H.A. *et al.* (1983), Robson (2000a), Rose (1997), Saunders & de Rebeira (1985), Saunders & Wooller (1988), Schodde (1977), Schodde & Mason (1976), Schodde & Tidemann (1986), Schodde *et al.* (1983), Secker (1951), Seitre & Seitre (1991), Simpson & Day (1998), Sitte & Jones (1994), Smythies (1999), St. Paul & McKenzie (1977), Stead (1932), Strahan (1994), Taylor (1966), Thompson (1984), Tolhurst (1987), Tronson & Tronson (1987), Tyler (1961), Varghese (1977), Wardill (1995), Watling (1982), White & Bruce (1986), Williams (1975), Woinarski *et al.* (1988).

## 52. Cinnamon-banded Kingfisher

### *Todiramphus australasia*

**French:** Martin-chasseur couronné **German:** Timorliet **Spanish:** Alción de la Sonda  
**Other common names:** Timor Sunda/Lesser Sundas/Cinnamon-backed/Cinnamon-collared Kingfisher

**Taxonomy.** *Alcedo australasia* Vieillot, 1818, no locality = Timor.

Genus often merged into *Halcyon*. Forms a superspecies with *T. sanctus*, *T. tutus*, *T. veneratus*, *T. gambieri* and *T. godeffroyi*; has at times been considered conspecific with *T. sanctus*. Race *interpositus* included in *dammerianus* by some authors; *tringorum* possibly better lumped with nominate, as reckoned to be unstable and hybrid. Five subspecies tentatively recognized.

#### Subspecies and Distribution.

*T. a. australasia* (Vieillot, 1818) - Lombok, Sumba, Wetar and Timor (Lesser Sundas).  
*T. a. tringorum* (Hellmayr, 1914) - Romang (E Lesser Sundas).  
*T. a. dammerianus* (Hartert, 1900) - Damar and Babar (E Lesser Sundas).  
*T. a. interpositus* (Hartert, 1904) - Leti and Moa (E Lesser Sundas).  
*T. a. odites* (J. L. Peters, 1945) - Tanimbar Is.



**Descriptive notes.** 21 cm; male 28–58 g, female 39–55 g. Male nominate race rufous lores and eyebrow, dark green crown, black mask; dark green upperparts, bluer rump, wings and tail; light rufous collar and underparts; upper mandible blackish, lower mandible pale yellow with darker tip; iris dark brown; legs and feet blackish. Distinguished from *T. chloris* by rufous forehead, eyebrow, collar and underparts. Female slightly duller than male. Juvenile like female, but white tip to bill, black mottling on breast and flank, buff tips to upperwing-coverts. Races vary mainly in the colour and extent of green on crown: *odites*

like nominate but smaller, paler, crown bluer; *tringorum* rufous forecrown; *dammerianus* crown mostly rufous with small dark central patch; *interpositus* like previous but paler. Voice. Rapid trill, sometimes rising initially, always descending at end, 2–3 seconds long; series of 3–12 rapid, weak notes, “ch-w’hee, ch-w’hee”, 5–12 seconds long; also brief yapping notes.

**Habitat.** Primary and tall secondary forest, forest edge, monsoon woodland, open forest, also woodland and groves of shade trees in villages and cultivated lands; appears to require habitat with closed canopy; from sea-level to 700 m.

**Food and Feeding.** Insects and their larvae. Perches at various levels in the forest; probably takes prey from the ground.

**Breeding.** No information available.

**Movements.** Probably sedentary.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Restricted-range species: present in Northern Nusa Tenggara EBA, Sumba EBA, Timor and Wetar I:BA and Banda Sea Islands EBA. Generally uncommon, with fragmented distribution; locally more common in some areas, e.g. interior of Sumba. Loss and degradation of habitat likely to have serious adverse effects, and the species is potentially vulnerable. More information on its biology, ecology and status urgently required.

**Bibliography.** Andrew (1992), Bishop & Brickle (1999), Coates & Bishop (1997), Collar & Andrew (1988), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Inskipp *et al.* (1996), Johnson & Stattersfield (1990), Jones, Jahaeni *et al.* (1994), Jones, Linsley & Marsden (1995), Knowles & Ntichen (1995), Linsley *et al.* (1999), Mayr (1944), Mees (1964), Mountfort (1988), Noske (1995), Rensch (1931), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Sujatnika *et al.* (1995), White & Bruce (1986).

## 53. Chattering Kingfisher

### *Todiramphus tutus*

**French:** Martin-chasseur respecté **German:** Boraboraliest **Spanish:** Alción Respetado  
**Other common names:** Pacific/Polynesian/Bora Bora/Respected/South Pacific Kingfisher, Leeward Island Kingfisher, Mangaia Island Kingfisher (*ruficollaris*)

**Taxonomy.** *Alcedo tuta* J. F. Gmelin, 1788, Tahiti.

Genus often merged into *Halcyon*. Forms a superspecies with *T. sanctus*, *T. australasia*, *T. veneratus*, *T. gambieri* and *T. godeffroyi*. Species name often given as *tuta*, but is Latinized Greek adjective and must agree with masculine genus name. Taxonomy of this group uncertain, and species boundaries not clear. Race *ruficollaris* often considered a separate species mainly on account of differences in vocalizations and greater development of rufous in plumage, though latter seems to represent the extreme of a range of plumage variation; on data currently available, probably better regarded as a race of present species, or possibly even of *T. sanctus*; due to erroneous placement of *Alcedo azurea ruficollaris* in *T. sanctus* in past, name *ruficollaris* for Mangaia birds was thought to be preoccupied and a replacement name, *mangaia*, published, but *ruficollaris* is available and valid and has priority. Extinct nominate race of *T. gambieri* sometimes placed within present species on basis of morphological criteria, but on limited information presently available it is probably better combined with the other Tuamotu taxon, *gertrudae*, in a separate species. Races *marinus*, *sacer*, *manuae* and *pedelei* of *T. chloris* might actually belong in present species. Detailed genetic research required to clarify these taxonomic problems, but this is hampered by scattered distribution of the various populations over thousands of kilometres of Pacific Ocean. Four subspecies currently recognized.

#### Subspecies and Distribution.

*T. t. tutus* (J. F. Gmelin, 1788) - Tupai, Maupiti, Bora Bora, Tahaa, Raiatea, Huahine and Tahiti (Society Is).

*T. t. atiu* (Holyoak, 1974) - Atiu (SE Cook Is).

*T. t. mauke* (Holyoak, 1974) - Mauke (SE Cook Is).

*T. t. ruficollaris* (Holyoak, 1974) - Mangaia (SE Cook Is).



**Descriptive notes.** 22 cm. Both sexes of nominate race have white forehead and supercilium, green and black mask, green-blue crown, back, wings and tail, white collar and underparts; upper mandible black, lower mandible pale yellow to ivory with dark cutting edges and tip; iris dark brown; legs and feet black. Distinguished from *T. veneratus* by white supercilium stripe and collar. Juvenile similar to adult, but buff margins to wing-coverts, black markings on hindneck and mantle, also breast with fine black barring, unlike black streaking of juvenile *T. veneratus*. Race *ruficollaris* has orange eyebrow, collar and sides of breast,

in female extending across breast; *atiu* has crown mainly white with green streaks and patch more limited to the central portion; *mauke* has forehead, collar and sides of breast washed buffy. Voice. Rapid, repeated “kee-kee-kee-kee” which sometimes runs into rattling chatter, also “ke-kow, ke-kow, ke-kow”, and various shrieks, cackles and chuckles; alarm a loud “shrii”; in *ruficollaris* contact or territorial call a loud “kek-kek-kek-kek”, also short note followed by more prolonged one “ki-wow ki-wow ki-wow” as loud contact call or quiet courtship call, also harsh “scark” as alarm, “chucka-chucka” as close contact call, twittering “tui-tui” as intimate contact, reaching crescendo at copulation, and also associated with visits to nest-hole or change-overs; nestlings make churring sounds.

**Habitat.** Primary forest, especially highland stream valleys, secondary forest, old plantations, cultivated land with trees, and gardens. Race *ruficollaris* on Mangaia I mainly in forest on raised circular platforms of coral limestone (makatea), with preference for unbroken canopy; most common in *Barringtonia asiatica* forest and other indigenous forest than in secondary forest, and absent from coastal shrubland.

**Food and Feeding.** Insects, including grasshoppers (Orthoptera), termites (Isoptera), stick-insects (Phasmida), cockroaches (Blattodea), moths and their larvae; also spiders, worms (Oligochaeta), freshwater shrimps 5–6 cm in length, small freshwater fish, and small lizards. Lizards important in diet on Mangaia I. Forages from middle and upper levels of trees; takes prey in flight, in or above the canopy, or from trunks, branches and in the foliage; also flies down to take prey on the ground or in shallow water.

**Breeding.** Lays in Dec-Jan in Society Is, in Nov-Jan on Mangaia. Following details for Mangaia race *ruficollaris*. Breeds as pairs, or as trios (15%) containing either 2 males or 2 females; in trios, both males copulated several times with female, suggesting polyandry. Territorial, birds call from treetops with bill pointed vertically; courtship feeding and copulation increased after nest-building, continued into incubation phase. Nest excavated by pair or trio in rotten trunk of *Hibiscus* or *Cocos* tree, in decaying limb of other living tree (*Barringtonia*, *Albizia*, *Hernandia*) or in tree cavity, 1.5–10 m above ground; many trees have several holes, up to 23 in a coconut stump; entrance hole 4.5 cm in diameter, with short tunnel and enlarged nest-chamber. Clutch 2–3 eggs, laid on successive days, all 3-egg clutches were from trios; incubation period 21–23 days, all adults incubating in bouts averaging 42 minutes; all feed and brood the young; fledging period c. 26 days. Presence of Common Mynas (*Acridotheres tristis*) at a nest considerably reduced feeding of the nestlings; eggs and chicks possibly preyed on by migrant Long-tailed Koel (*Eudynamis taitensis*).

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in Southern Cook Islands EBA and Society Islands EBA. Race *ruficollaris* on Mangaia I Vulnerable. Common or abundant on some islands, mainly remote ones with less human impact; rare and localized on Tahiti, also on Bora Bora, where apparently declining; almost certainly extinct on Tupai I. Habitat destruction and the increasing human population the main causes of decreases. Race *ruficollaris* population 250–450 in 1992, reassessed at 400–700 in 2000; densities ranged from 0–41 birds/ha in *Barringtonia asiatica* forest and 0–37/ha in other indigenous forest to 0–21/ha in secondary forest; has declined as result of forest fragmentation and loss caused by clearance for agriculture, and browsing by goats; also faces competition for food and nesting sites from introduced Common Myna, and possibly preyed on by introduced cats and rats (*Rattus*).

**Bibliography.** Berlioz (1938), Collar & Andrew (1988), Collar *et al.* (1994), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Holyoak (1974b, 1974c, 1980), Holyoak & Thibault (1984), Knowles & Ntichen (1995), McCormack (1997), Mountfort (1988), Pratt *et al.* (1987), Rowe & Empson (1996a, 1996b), Schodde & Holyoak (1977), Schodde & Mason (1976), Seitre & Seitre (1991), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Steadman (1985, 1988), Steadman & Kirch (1990), Thibault & Thibault (1975).



## 54. Tahiti Kingfisher

### *Todiramphus veneratus*

**French:** Martin-chasseur vénéré **German:** Tahitilist **Spanish:** Alción Venerado  
**Other common names:** Venerated Kingfisher

**Taxonomy.** *Alcedo venerata* J. F. Gmelin, 1788, Society Islands. Genus often merged into *Halcyon*. Forms a superspecies with *T. sanctus*, *T. australasia*, *T. tutus*, *T. gambieri* and *T. godeffroyi*. Two subspecies recognized.

**Subspecies and Distribution.**  
*T. v. veneratus* (J. F. Gmelin, 1788) - Tahiti (Society Is).  
*T. v. youngi* Sharpe, 1892 - Moorea (Society Is).



**Descriptive notes.** 21 cm. Male nominate race blue-green upperparts, browner on forehead and crown; white underparts, variable broad pale rufous breastband often broken in centre; upper mandible black, lower mandible horn with black cutting edges and tip; iris dark brown; legs and feet black. Distinguished from *T. tutus* by breastband, no white eyebrow or collar. Female duller upperparts, blackish breastband. Juvenile browner upperparts, black streaking on lower throat and breastband, buffy flanks and belly. Race *youngi* slightly larger, pale brown upperparts, white underparts except for dusky fringes to neck and breast. Voice.

Calls frequently, particularly at dawn and before dusk; rattling "ki-ki-ki-ki-ki", also high double-note whistle, and various raucous croaks and cries.

**Habitat.** Primary and secondary forest at up to 300 m on Moorea and montane forest at up to 1700 m on Tahiti, in *Purao* woodland, also plantations and gardens. Occurs alongside *T. tutus*, with no overlap of territories.

**Food and Feeding.** Insects and their larvae, fish, crustaceans, and small lizards. Sits on a conspicuous perch in middle to upper levels of the canopy, watching for prey; food taken from the ground, but insects also caught in flight or among foliage; will dive into shallow water for aquatic prey.

**Breeding.** Lays in Oct-Dec on Tahiti. Nest excavated in rotting branch or tree trunk, up to 11 m above ground. Clutch 3 eggs. No other information.

**Movements.** Probably sedentary.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in Society Islands EBA. Widespread and common on Tahiti; generally uncommon on Moorea, but at some localities somewhat more common. No known threats, but in some areas habitat loss or degradation must be a potential threat, at least in the future.

**Bibliography.** Berlioz (1938), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Holyoak (1974c), Holyoak & Thibault (1984), Knowles & Nitcher (1995), Pratt *et al.* (1987), Seitre & Seitre (1991), Stattersfield *et al.* (1998), Thibault (1988), Thibault & Rives (1988), Wheatley (1998).

## 55. Tuamotu Kingfisher

### *Todiramphus gambieri*

**French:** Martin-chasseur des Gambier **German:** Tuamotulist **Spanish:** Alción de la Niau  
**Other common names:** Mangareva Kingfisher (*gambieri*); Niau Kingfisher (*gertrudae*)

**Taxonomy.** *Halcyon gambieri* Oustalet, 1895, Mangareva, in Gambier Islands, Tuamotu Archipelago.

Genus often merged into *Halcyon*. Forms a superspecies with *T. sanctus*, *T. australasia*, *T. tutus*, *T. veneratus* and *T. godeffroyi*. Taxonomy unclear, and much disputed: extinct nominate race often considered a race of *T. tutus*, with race *gertrudae* then usually treated as a separate species, on basis of plumage differences and wide geographical separation from nominate; plumage characteristics have been used to support lumping of nominate *gambieri* with *T. tutus*, as it is intermediate between races *tutus* and *ruficollaris* of that species, but these last two races are geographically very much closer to each other than either is to supposedly intermediate *gambieri*, making this interpretation an unlikely one; conceivably, *gambieri* and *gertrudae* might constitute two separate full species, or might even both be races of *T. tutus*, but limited information available suggests the treatment followed herein as the best option, at any rate for the present; doubts have also been expressed regarding the type locality of Mangareva, and it has been suggested that the single specimen might actually have come from Micronesia; much research still required, and particularly DNA analyses of the many taxa involved, to enable a detailed taxonomic review to be made. One extant subspecies recognized.

**Subspecies and Distribution.**

*T. g. gertrudae* Murphy, 1924 - Niau (W Tuamotu Is).



**Descriptive notes.** 20 cm. Race *gertrudae* has buffy head and neck, blue on crown of variable extent, blue line leading back from eye; blue or green-blue upperparts with darker purple wash on wings and tail; pale orange to cream on sides of neck and breast; upper mandible black, lower mandible pale pinkish-apricot to yellow, with blackish edges and tip; iris dark brown; legs and feet black. Juvenile undescribed. Voice. Not described.

**Habitat.** Woodland, coconut plantations and village gardens; occasionally in forest.

**Food and Feeding.** Insects and larvae, e.g. beetles; also small lizards. Reported also to

catch small fish in reef ponds at low tide.

**Breeding.** Lays in Sept, possibly also in May-Jun. Excavates cavity in dead coconut tree or in rotting coconut attached to tree; report of nest consisting of grass and stems in coconut palm requires confirmation. No other information.

**Movements.** Presumed to be sedentary.

**Status and Conservation.** VULNERABLE. Nominative race probably became extinct on Mangareva 1 before 1922. Surviving race *gertrudae* restricted to a single island just 26 km<sup>2</sup> in size, but reasonably secure there. Population estimated to be 400-600 individuals in 1974, and reported as common

in 1990. Suggestions have been made to translocate populations to adjacent islands. Whether rats (*Rattus*) are present on Niau is unknown; presence of such mammals, and introductions of other species, could pose serious problems for this species. More information on its biology and status is urgently required.

**Bibliography.** Berlioz (1938), Bruner (1972), Collar & Andrew (1988), Collar *et al.* (1994), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Green & Hiron (1991), Holyoak & Thibault (1977, 1984), Knowles & Nitcher (1995), Lacan & Mougin (1974), Mountfort (1988), Murphy (1924), Seitre, J. & Seitre (1991), Seitre, R. & Seitre (1992), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Thibault (1973, 1988), Tomlinson (2000).

## 56. Marquesas Kingfisher

### *Todiramphus godeffroyi*

**French:** Martin-chasseur des Marquises **Spanish:** Alción de las Marquises  
**German:** Marquesasliet

**Taxonomy.** *Halcyon godeffroyi* Finsch, 1877, Marquesas Islands.

Genus often merged into *Halcyon*. Forms a superspecies with *T. sanctus*, *T. australasia*, *T. tutus*, *T. veneratus* and *T. gambieri*. Monotypic.

**Distribution.** Hiva Oa and Tahuata, in Marquesas Is; reports from other islands in Marquesas (Ua Pou, Mohotani and Fatu Hiva) are apparently erroneous.



**Descriptive notes.** 21 cm. Both sexes white crown, neck and underparts, dark mask through eye continuing as blue-black stripe and as thin band across nape; upper mantle with characteristic buffy triangle, rest of upperparts, wings and tail bright blue; upper mandible black, lower mandible pale yellow to pale horn, with dark tip and cutting edges; iris dark brown; legs and feet black. Juvenile blue-green crown, black side of head and across breast, green-blue upperparts. Voice. Short, deep, repeated "kiau", which can accelerate into chatter; also soft "treet-tee-tee".

**Habitat.** Primary forest, preferring dense humid forest along mountain streams and in remote valleys; observed also in coconut plantations, on dry slopes with mango and *Eugenia cumini* trees, and on peaks covered with *Casuarina* groves. Lowlands to middle altitudes.

**Food and Feeding.** Insects, mainly beetles (Coleoptera) and large grasshoppers (Orthoptera), and small lizards; possibly some fish. Takes prey in the foliage, or by swooping to the ground or water from a perch.

**Breeding.** Lays in Sept-Jan on Hiva Oa. Nest found in hole of old mango tree, another in hollow with 2 entrances dug into decayed screw-pine (*Pandanus*) trunk, site 2-5 m above ground, nest-hole diameter 3-5 cm. No other information.

**Movements.** Presumably sedentary.

**Status and Conservation.** ENDANGERED. Restricted-range species: present in Marquesas Islands EBA. Population in 1970's 300-500 pairs on Tahuata and under 50 pairs on Hiva Oa; on latter island extremely rare in 1990, but found to be still surviving there in February 2000, although situation regarded as critical; apparently declining on Tahuata. Has suffered from extensive habitat damage caused by feral livestock. Introductions of Great Horned Owl (*Bubo virginianus*) and Common Myna (*Acridotheres tristis*), as well as black rat (*Rattus rattus*), have been blamed for its decline on Hiva Oa, and perhaps also on Tahuata, but these animals have been present on islands since earlier decades of 20th century. Possibly other factors, as yet unidentified, are responsible for this kingfisher's parlous situation.

**Bibliography.** Adamson (1939), Berlioz (1938), Collar & Andrew (1988), Collar *et al.* (1994), Ehrhardt (1978), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Green & Hiron (1991), Holyoak (1975), Holyoak & Thibault (1984), Knowles & Nitcher (1995), Mountfort (1988), duPont (1976b), Pratt *et al.* (1987), Seitre, J. & Seitre (1991), Seitre, R. & Seitre (1992), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Thibault, B. & Thibault (1973), Thibault, J.C. (1988), Tomlinson (2000).

## 57. Red-backed Kingfisher

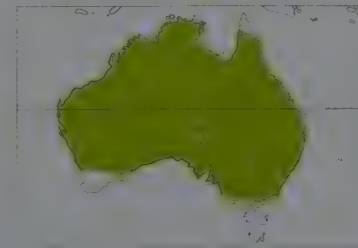
### *Todiramphus pyrrhopygius*

**French:** Martin-chasseur à dos de feu **German:** Rotbürzellist **Spanish:** Alción Culirrijo  
**Other common names:** Golden/Red-rumped Kingfisher

**Taxonomy.** *Halcyon pyrrhopygia* Gould, 1841, interior of New South Wales.

Genus often merged into *Halcyon*. Monotypic.

**Distribution.** Australia, except extreme SW and Tasmania.



**Descriptive notes.** 22 cm; male 45-70 g, female 41-62 g. Smallish kingfisher with distinctive streaky green crown, and rufous lower back and rump. Male white forehead and eyebrow, blackish mask extending across nape, white collar and underparts, dark green mantle, blue wings and tail; upper mandible blackish, lower mandible pale yellow to ivory from base, with darker tip; iris dark brown; legs and feet black. Female like male, but duller colours, and somewhat buffier wash on collar and flanks. Juvenile like female, but more obvious rufous-buff on hindneck and flanks, dusky tips to neck and breast feathers. Voice. Single downward-inflected note, "pee-eee", may be repeated every 3 seconds in long series; alarm either a whistle or a harsh chattering call; churring call by adults feeding young at nest.

**Habitat.** Most common in arid or semi-arid zones and seasonally dry tropics with open woodland, mallee, open mulga, *Acacia* scrubland and coolabah-lined riverbeds, spinifex and tussock grassland with some trees; sometimes near coast, fringes of open *Melaleuca* swamp-woodland, and rarely at edges of monsoon forest. Often seen on powerlines along roads, or crossing open floodplains; often enters suburbs.

**Food and Feeding.** Locusts and grasshoppers (Orthoptera), leaf insects (Phasmida), mantids (Mantodea), beetles (Cerambycidae, Dytiscidae, Scarabaeidae, Tenebrionidae), bugs (Nepidae,



Notonectidae), ants (Formicidae), caterpillars, mole-cricket (Gryllotalpidae), also spiders, centipedes (Chilopoda), crustaceans, scorpions (Scorpiones); vertebrates, including fish, frogs and tadpoles, lizards (Agamidae, Scincidae, Gekkonidae), small snakes, and mice (*Mus musculus*). Also seen to attack nesting colony of Fairy Martins (*Hirundo ariel*) to take eggs and nestlings. Sits on fairly exposed perch, often overhead wires and fences; swoops to ground for prey, which is then carried back to perch. Also takes food from trunks of trees. Height of dives 3-40 m, horizontal distance 0-30 m, 47% of dives successful.

**Breeding.** Lays in Aug-Feb in N Australia, in Sept-Feb in S; breeds opportunistically in C Australia, continuously in abnormally wet years; normally double-brooded. Calling and displays of red rump accompany courtship feeding; migrants arriving at breeding areas call continually during day. Nest excavated by both of pair in vertical bank of a river, creek or dam, or in earth cliff, sandy bank or mine shaft, or in terrestrial or arboreal termitarium (particularly mound of magnetic termite *Amitermis*), or in earth among roots of uprooted tree; very occasionally in natural tree hollow, haystack or hole in a water pipeline; record of nesting in colony of White-backed Swallows (*Cheramoeca leucosternus*); nest entrance averages 2 m (0.8-10 m) from ground, or 1.8 m (0.2-20 m) from top of a bank 3-4 m (0.6-30 m) tall; burrow averages 28 cm long (up to 120 cm) and 6 cm in diameter, ending in nest-chamber 16 cm in diameter and 16 cm high; once, tunnel diameter reduced by a plug of dirt and saliva, possibly to conceal young from predators; nest-tunnels frequently reused. Clutch 2-6 eggs, normally 4-5; both sexes incubate, period 20-23 days; both also feed young, which are probably not brooded; fledging period 26-30 days; second brood started while still feeding young from first. Nest failure from heavy rain entering burrow, also from goannas (*Varanus*), dingoes and foxes (*Vulpes*) digging into nest-chamber and eating contents and sometimes a parent as well.

**Movements.** In S parts of range seems to be largely a migrant, moving S in austral summer (Aug-Apr) to breed, then returning N in winter; some birds remain all year in S. In N Australia recorded all year, with numbers in post-breeding period boosted by migrants from S. In other areas there seems to be a movement to the coast in non-breeding season. In many areas its presence is nomadic, with no definite pattern, and is probably related to erratic rainfall patterns.

**Status and Conservation.** Not globally threatened. Although sparsely distributed, it is widespread in Australia in a variety of dry habitats. Density of 0.01 birds/ha in Northern Territory, and 19 counted in 132-km drive near Alice Springs. Has benefited from road construction in mallee: trees were knocked over, leaving soil around their roots, this providing nesting sites for this kingfisher. **Bibliography.** Andrew & Rogers (1993), Barker & Vestjens (1989), Blakers *et al.* (1984), Brooker *et al.* (1979), Chinner (1977), Courtney (1971b), Crawford (1972), Eastman (1970), Eckert (1989), Frith & Hitchcock (1974), Gosper & Gosper (1996), Hall (1974), Higgins (1999), Hobbs (1961, 1962, 1976), Horton (1975), Johnstone & Storr (1998), Johnstone, Dell *et al.* (1977), Johnstone, de Rebeira & Smith (1979), Jurisevic & Sanderson (1994), Lindsey (1992), Longmore (1978), Lord (1935), Macdonald (1988), McBride & Dampney (1982), Pizzey & Knight (1977), Rix (1970), Roberts (1979), Rose (1997), Schmidt (1978), Schodde & Tidemann (1986), Serventy & Whittell (1976), Simpson & Day (1998), Slater & Lindgren (1955), Storr (1973, 1977, 1980), Strahan (1994), Thompson (1984), Tronsson & Tronsson (1987), Van Horne (1987), Woinarski & Tidemann (1991).

## Genus SYMA Lesson, 1827

### 58. Yellow-billed Kingfisher

#### *Syma torotoro*

**French:** Martin-chasseur torotoro **German:** Gelbschnabellist **Spanish:** Alción Torotoro  
**Other common names:** Lesser Yellow-billed/Lowland/Lowland Yellow-billed/Saw-billed Kingfisher

**Taxonomy.** *Syma torotoro* Lesson, 1827, Manokwari, New Guinea.

Genus sometimes merged into *Halcyon*, or occasionally even into *Todiramphus*. Forms a superspecies with *S. megarhyncha*, with which has possibly hybridized. Birds from SE New Guinea formerly awarded race *meeki*, but now considered inseparable from nominate; other forms now subsumed into nominate include *tentelare* of Aru Is. and *pseustes* and *brevirostris* both of SC New Guinea. Three subspecies currently recognized.

#### **Subspecies and Distribution.**

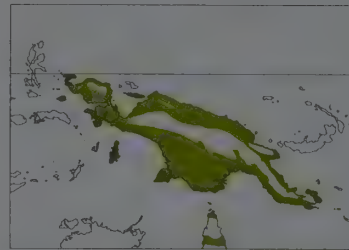
*S. t. torotoro* Lesson, 1827 - lowland New Guinea, W Papuan Is. Yapen I and Aru Is.

*S. t. ochracea* Rothschild & Hartert, 1901 - D'Entrecasteaux Is.

*S. t. flavirostris* (Gould, 1850) - NE Australia in Cape York Peninsula (S to Weipa and Massy Creek).

**Descriptive notes.** 20 cm; male 32-50 g, female 30-52 g. Distinctive small kingfisher with yellow bill; often holds crown feathers raised. Male of nominate race has rufous head, paler rufous underparts; black patch on nape; back, rump and uppertail-coverts greenish-blue, tail dark blue; flight-feathers black with bluish-green edges and tips; bill bright yellow, serrated edges towards tip of upper mandible; iris dark brown; legs and feet yellow. Distinguished from very similar *S. megarhyncha* by smaller size, no dark line on culmen. Female has dark crown patch, 2 neck patches joined by a line, paler underparts. Juvenile like female, but rufous edges to black crown feathers, more black around eye, dusky tips to cheek and breast feathers, grey-black bill. Race *ochracea* larger, darker below, female larger dark patch on crown; *flavirostris* paler overall, adults retain some black on culmen. **VOICE.** Loud, clear, short trill lasting 1-2 seconds, descending slightly and ending abruptly, or long trill 5-6 seconds, initially like short trill but then constant pitch while loudness decreases; sometimes preceded by single, short sharp notes which then accelerate into main call; may counter-sing, using different variants of call; screams when attacking intruder; also mutual chatters, rarely a kookaburra-like laugh.

**Habitat.** Primary and secondary rainforest, monsoon, gallery, vine and mangrove forest, mature teak and rubber plantations, monsoon scrub, forest clearings and edges; will use isolated patches of forest surrounded by woodland or sclerophyll forest, and often seen along roads through forest, at forest edges or ecotones. In New Guinea, 58% of observations in understorey less than 8 m from ground, 29% in subcanopy at 8-25 m, and only 11% in canopy or upper canopy above 25 m;



with an audible thump. Observations of feeding in New Guinea showed that most prey (73%) taken on the ground, 18% from foliage, and 9% in the air. Occasionally hunts at the water's edge, or by digging in leaf litter and topsoil.

**Breeding.** Lays in Nov-Jan in Cape York Peninsula; in Aug-Mar in Papua New Guinea. Much singing and aggression at start of breeding season, suggesting territorial habit. Nest excavated by both sexes, usually in active arboreal termitarium (*Eutermes*) but occasionally in tree hollow, 3-15 m above ground; one nest had entrance 4 cm wide and 4 cm long, leading to chamber 12 cm deep, 9 cm wide and 9.5 cm high; chamber sometimes lined with wood dust or debris from termitarium. Clutch 3-4 eggs in Queensland, 1-4 in Papua New Guinea; both sexes defend nest, incubate eggs and attend nestlings; no information on incubation and fledging periods.

**Movements.** Sedentary; all 24 recoveries of ringed birds were less than 10 km from ringing site; in Papua New Guinea, 6 ringed birds were recaptured 2 years later within 100 m of original ringing site. **Status and Conservation.** Not globally threatened. Widely distributed and quite common, particularly at lower altitudes. Occurs in Varirata National Park, in Papua New Guinea. Density near Port Moresby (Papua New Guinea) was estimated at 1 bird/ha; on Cape York Peninsula central points of territories were c. 250 m apart on edge of monsoon forest.

**Bibliography.** Andrew (1992), Bailey (1992), Barker & Vestjens (1989), Barnard (1911), Beehler (1978), Beehler *et al.* (1986), Bell (1970b, 1970c, 1979, 1981, 1982b, 1984a, 1984b), Beruldsen (1979, 1990), Blakers *et al.* (1984), Coates (1985), Diamond (1972), Draffan *et al.* (1983), Finch (1982), Frith & Frith (1993), Gilliard & LeCroy (1966, 1967a), Greenway (1935), Gregory (1995a), Gyldenstolpe (1955b), Higgins (1999), Lindsey (1992), Macdonald (1988), MacGillivray (1914, 1918, 1932), Mackay (1970), Mayr & Rand (1937), Mees (1965, 1982), Pearson (1975b), Peckover & Filewood (1976), Pizzey & Knight (1997), Rand (1938, 1942a), Rand & Gilliard (1967), Ripley (1964), Schodde & Tidemann (1986), Simpson & Day (1998), Strahan (1994), Tronsson & Tronsson (1987), Weston (1975).

### 59. Mountain Kingfisher

#### *Syma megarhyncha*

**French:** Martin-chasseur montagnard **German:** Berglist **Spanish:** Alción Montano  
**Other common names:** Greater Yellow-billed/Mountain Yellow-billed Kingfisher

**Taxonomy.** *Syma megarhyncha* Salvadori, 1896, Moroka, New Guinea.

Genus sometimes merged into *Halcyon*, or occasionally even into *Todiramphus*. Forms a superspecies with *S. torotoro*, and there are some possible hybrids between the two species. Three subspecies recognized.

#### **Subspecies and Distribution.**

*S. m. wellsi* Mathews, 1918 - W New Guinea, in Snow Mts and Weyland Mts.

*S. m. sellamontis* Reichenow, 1919 - NE New Guinea, in mountains of Huon Peninsula.

*S. m. megarhyncha* Salvadori, 1896 - C & SE New Guinea, from Sudirman Range to Owen Stanley Range.



**Descriptive notes.** 24 cm; male 52-60 g, female 49-63 g. Male nominate race has rufous head and underparts, black loreal patch, black nape patch, greenish-blue upperparts, dark blue tail, black wing feathers with bluish edges and tips; bill bright yellow, dusky ridge along culmen, serrated edges at tip of upper mandible; iris dark brown; legs and feet dull yellow. Differs from very similar *S. torotoro* in larger size, larger black spot in front of eye, dark on culmen. Female black crown, black neck patches joined across hindneck, paler underparts. Juvenile grey-black bill, larger black area around eye, dusky-tipped feathers on cheeks

and breast. Race *wellsi* slightly larger and darker than nominate, but shorter-billed; *sellamontis* slightly smaller, bill totally yellow. **VOICE.** Loud trilling call, lasting several seconds, seems identical to that of *S. torotoro*.

**Habitat.** Primary forest and secondary growth, mainly between 1200 m and 2200 m, occasionally down to 760 m. Replaced at lower altitudes by *S. torotoro*.

**Food and Feeding.** Insects, larvae, and small lizards. Perches for long periods in middle and upper canopy, before diving for prey in the foliage or on the ground.

**Breeding.** Lays in Dec in Papua New Guinea. Nest-site a hole in an earth bank or a hole in tree. Clutch 2 eggs; no information on incubation and fledging periods.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Locally common, but generally scarce. Rather little-known species; more information is required on its biology.

**Bibliography.** Andrew (1992), Beehler (1978), Beehler *et al.* (1986), Clapp (1987), Coates (1985), Diamond (1972), Finch (1979, 1981c), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Gregory (1995a), Gyldenstolpe (1955b), Harrison & Frith (1970), Knowles & Ntchen (1995), Mackay (1980, 1991), Majnep & Bulmer (1977), Mayr & Gilliard (1954), Mayr & Rand (1937), Rand (1942b), Rand & Gilliard (1967), Ripley (1964), Wahlberg (1988), Weston (1976).







PLATE 17

inches 3  
cm 7



## Subfamily ALCEDININAE

### Genus *CEYX* Lacépède, 1799

#### 60. African Dwarf-kingfisher

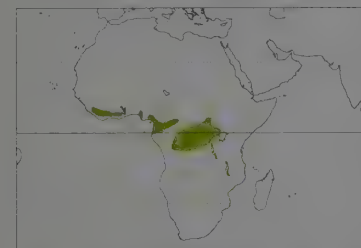
##### *Ceyx lecontei*

**French:** Martin-pêcheur à tête rousse **Spanish:** Martín Pímeo del Congo  
**German:** Braunkopf-Zwergfischer  
**Other common names:** Red-headed Dwarf-kingfisher, Black-fronted Pygmy-kingfisher

**Taxonomy.** *Ispidina Lecontei* Cassin, 1856, Moonda River, Gabon. Sometimes placed in genera *Corythornis* or *Ispidina*; alternatively in nonspecific *Myioceyx*. Closely related to *C. pictus*. Ugandan birds described as race *ugandae*, but inseparable from nominate. Two subspecies recognized.

##### **Subspecies and Distribution.**

*C. l. ruficeps* (Hartlaub, 1857) - Liberia E to Ghana.  
*C. l. lecontei* (Cassin, 1856) - SW Nigeria through Cameroon to W Gabon, and from Congo Basin to W Rift Valley and SW Uganda; isolated records from R Congo mouth, N Angola and SW Sudan.



**Descriptive notes.** 10 cm; male 9-11 g, female 9-5-12 g. Tiny kingfisher. Both sexes of nominate race have rufous head, black forehead, tiny iridescent blue tips to crown feathers, white chin and throat; blue-black back, wings and tail; rufous underparts; bill with curious square tip, orange-red; iris dark brown; legs and feet orange-red. Juvenile has black feathers with blue tips on crown, upperwing-coverts and mantle, bill black with white tip and red base to lower mandible. Race *ruficeps* smaller, lacks iridescent blue spots on crown. **VOICE.** High-pitched squeak.

**Habitat.** Primary rainforest, often along streams, also dense undergrowth in riverine forest, secondary growth at forest edges; sometimes more open areas, such as waterlogged oil palm (*Elaeis guineensis*) plantations and clearings in forest.

**Food and Feeding.** Insects, including damselflies (Odonata), mantises (Mantodea), beetles (Coleoptera) and their larvae, ants (Formicidae), large flies (Diptera). Sits on a low perch, 1-2 m above ground, and takes prey from the ground or in air; sometimes takes insects disturbed by ant columns.

**Breeding.** Lays in Feb in Cameroon, in Nov-Mar in Gabon, and in Sept-Nov in NW Zaïre. During courtship pair-members face each other, bill pointing almost vertically, and sing in duet; male then flies around female several times, then rapidly in a tight circle around her, perches and sings again. Nest in a low earth bank or wall of an earth pit, chamber 5 cm high, at end of a 15-cm burrow. Clutch 3 eggs; incubation and fledging periods undocumented; 2 weeks after hatching nestling's eyes partly open, feathers largely sheathed, at 3 weeks eyes fully open and nestling fully feathered; nest-cavity becomes littered with insect remains.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Has wide distribution. Although considered uncommon over much of its range, it is reported as locally common in Gabon, and common in the forests of Bwamba, Budongo and Lugalambo in Uganda.

**Bibliography.** Allport *et al.* (1989), Bannerman (1933, 1953), Bates (1911, 1930), Bertioz (1962), Bouet (1961), Britton (1980), Brosset (1976), Chapin (1939), Christy & Clarke (1994), Clancey (1992), Colston & Curry-Lindahl (1986), Dean (2000), Dekeyser & Derivot (1966), Dickerman (1993), Dowsett (1989b), Dowsett & Dowsett-Lemaire (1991, 1993, 1997), Dowsett & Forbes-Watson (1993), Dowsett-Lemaire & Dowsett (1999, 2000), Elgood *et al.* (1994), Field (1999), Friedmann (1978), Friedmann & Williams (1971), Fry (1980a), Fry *et al.* (1988), Gartshore (1989), Gartshore *et al.* (1995), Gatter (1988, 1997), Germain & Cornet (1994), Grimes (1987), Heigham (1976), Hockey (1997), Lippens & Wille (1976), Louette (1981b), Mackworth-Præd & Grant (1957, 1962, 1970), Pinto (1983), Sergeant (1993), Serle *et al.* (1977), Short *et al.* (1990), Snow (1978), van Someren (1949), Tomlinson (2000), Traylor (1963), Traylor & Archer (1982).

#### 61. African Pygmy-kingfisher

##### *Ceyx pictus*

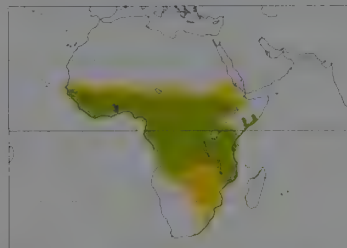
**French:** Martin-pêcheur pygmée **German:** Natalzwergfischer **Spanish:** Martín Pímeo Africano  
**Other common names:** Pygmy/Miniature Kingfisher

**Taxonomy.** *Todus pictus* Boddaert, 1783, Juida = St Louis, Senegal. Sometimes placed in *Corythornis* or *Ispidina*. Closely related to *C. lecontei*. Birds of S Somalia formerly separated as race *jubaensis*. Identity of birds breeding on Pemba unclear, as both nominate and *natalensis* have been collected there. Three subspecies recognized.

##### **Subspecies and Distribution.**

*C. p. pictus* (Boddaert, 1783) - Senegal E to Eritrea, S to Uganda and Pemba (possibly).  
*C. p. ferrugineus* (Clancey, 1984) - Guinea-Bissau E to W Uganda, S to C Angola, NW Zambia and N Tanzania.  
*C. p. natalensis* (A. Smith, 1832) - S Angola across to C & E Tanzania, including Pemba (possibly) and Zanzibar, and S to E Botswana and N & E South Africa; some migration N to E Zaïre, Uganda and S Sudan.

**Descriptive notes.** 12 cm; male 11-16 g, female 9-15 g. Both sexes nominate race black crown with glossy blue tips; rufous eyebrow and hindneck with distinctive lilac wash on side of head; dark purple-blue mantle, back and rump; wing-coverts black and blue, flight-feathers mostly black, tail black; chin and throat white, remaining underparts rufous. Iris dark brown; bill, legs and feet red. Juvenile



duller, blues paler, dusky barring on breast, black bill with yellowish tip. Race *ferrugineus* darker than nominate; *natalensis* broader orange eyebrow, blue spot on side of neck. **VOICE.** Thin, high-pitched "seek" or "tseet tseet", often in flight; also prolonged high twittering song, "chewtichichew chewtichéetew skitisee-see tseu-tseieu-chewtiseu tsip tseu tseu tseu...".

**Habitat.** Thick evergreen forest, riverine forest and swamp-forest, woodland, thickets and trees in dry thornveld and grassland, plantations, arable and pasture land, and large gardens. In Angola and E Africa, resident race *ferrugineus* is found in forest while migratory *natalensis* is

more often found in *Brachystegia* woodland.

**Food and Feeding.** Insects, including grasshoppers (Orthoptera), moths and caterpillars, flies (Diptera), beetles (Coleoptera); also spiders, small millipedes (Diplopoda), pill bugs (Oniscoidea); also aquatic invertebrates, and small frogs (*Hyla*) and lizards (Gekkonidae). Sits on a low perch 1 m from ground, scanning for prey, with occasional head-bobbing or tail-flipping; takes prey in flight, from the ground or from the surface of water, and returns to perch, where prey beaten on the branch before being swallowed head first. Sometimes follows columns of driver ants to catch fleeing insects.

**Breeding.** Lays in Sept-Nov in Mauritania and Mali, and in Mar-Oct in S parts of W Africa; in Jan, Mar-Jun and Oct-Nov in E Africa; in Jan-Mar and Aug-Oct in Zaïre and Angola; in Oct-Dec, occasionally to Mar, in S Africa; sometimes several broods raised in a season. Solitary or semi-colonial; more than 20 nests have been found in a 500-m length of bank in N Nigeria. Nest-tunnel 30-60 cm long, dug by the pair into streambank, erosion gully, ground termitarium or the side of aardvark (*Orycteropus afer*) burrow; one nest was in a bank 1 m above a stream, with tunnel 40 cm long and ending in nest-chamber 13 cm x 10 cm. Clutch 3-6 eggs (mean 3.8), larger clutches found away from equator; both sexes incubate and both feed the young; in captivity, incubation period was 18 days, young were fed 8 times per hour, 2 young fledged after 18 days and were independent 5 days later, when the pair laid a second clutch.

**Movements.** S populations present in South Africa and Zimbabwe from Oct to Apr/May, in Zambia Aug-May, and in Katanga, Zaïre, Sept-May; after breeding, migrate N to Rwanda (Mar-Aug), NE Zaïre (Apr-Aug), Uganda and Talanga, in S Sudan (Jun-Jul); some may overwinter in coastal Mozambique, South Africa and scattered localities in Zimbabwe. In S Malawi present all year, although summer and winter populations differ. N breeding populations are migratory N of 12-13° N, where present May-Nov; S of 9° N resident and partial migrant, some moving S to Zaïre and Burundi, where present Sept-Mar.

**Status and Conservation.** Not globally threatened. Has a wide distribution, and found in a range of habitats. Many are killed in Zimbabwe and South Africa by hitting buildings while migrating at night; more than 20 were killed on one night in Durban. This species has bred successfully in captivity.

**Bibliography.** Allport *et al.* (1989), Anon. (1998b), Ash & Miskell (1998), Balança & de Visscher (1997), Bannerman (1953), Barlow *et al.* (1997), Bates (1927), Benson (1982), Benson & Benson (1977), Benson *et al.* (1971), Bouet (1961), Britton & Britton (1974), Brunel (1958), Burton (1967), Cave & Macdonald (1955), Chapin (1939), Cheke & Walsh (1996), Chenuaux-Repond (1978), Christy & Clarke (1994), Clancey (1964a, 1964d, 1971a, 1972, 1984b, 1992, 1996), Colston & Curry-Lindahl (1986), Curry-Lindahl (1960), Dean (1971, 1974, 2000), Dekeyser & Derivot (1966), Dowsett (1988), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Duckworth *et al.* (1992), Elgood *et al.* (1973), Everitt (1964), Field (1999), Friedmann (1930a, 1978), Friedmann & Williams (1969, 1971), Fry (1965, 1980a), Fry *et al.* (1988), Gartshore (1989), Gatter (1988, 1997), Gee & Heigham (1977), Germain *et al.* (1973), Ginn *et al.* (1989), Giraudeau *et al.* (1988), Greig-Smith (1976), Grimes (1987), Hamner (1976, 1979, 1980b), Harrison *et al.* (1997), Harwin (1976, 1978, 1984a), Herremans (1994), Hockey (1997), Irwin (1978), Jackson (1972), Jones (1984), Kemp (1974), Lamareche (1988), Leonard (1998a), Lewis & Pomeroy (1989), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Morel & Morel (1990), Nikolaus (1979, 1987), Okia (1976), Pakenham (1979), Penry (1994), Pinto (1983), Postage (1983), Prigogine (1973), Quantrell & Quantrell (1998), Reid-Henry (1970), Rutgers & Norris (1977), Schönwetter (1966), Serle (1965, 1981), Serle *et al.* (1977), Short *et al.* (1990), Snow (1978), Traylor (1960a), Wilkinson (1982), Zimmerman *et al.* (1996).

#### 62. Oriental Dwarf-kingfisher

##### *Ceyx erithaca*

**French:** Martin-pêcheur pourpré **German:** Dschungelfischer **Spanish:** Martín Pímeo Oriental  
**Other common names:** Malay/Three-toed/Rufous-backed/Red-backed Kingfisher, Black-backed/Rufous-backed Dwarf-kingfisher, Malay Forest-kingfisher

**Taxonomy.** *Alcedo erithaca* Linnaeus, 1758, Bengal.

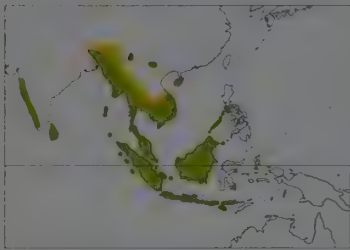
Forms a superspecies with *C. melanurus*. Distinctive rufous-backed form was, in past, widely considered a separate species, "*C. rufidorsa*"; this view was supported by the situation N of Kuala Lumpur (C Peninsular Malaysia), where there is little hybridization between rufous-backed and black-backed morphs and only the latter is migratory; on other hand, considerable hybridization occurs in Borneo, and also in Sumatra and S Peninsular Malaysia, with a wide range of intermediates, strongly suggesting that the two forms are merely morphs of a single species. Population on Sumatran islands of Simeulue and Batu sometimes separated as race *jungei* and that on Nias as race *capetus*, but both now seem better placed within nominate; birds of Mindoro have at times been further separated as race *vargasi*. Original species name *erithaca* is a noun, and therefore remains unchanged, irrespective of gender of genus in which placed. Three subspecies currently recognized.

##### **Subspecies and Distribution.**

*C. e. erithaca* (Linnaeus, 1758) - SW India (S from Bombay) S to Sri Lanka, and from Bhutan E to S China (Yunnan, Hainan) and S to Sumatra and adjacent islands.  
*C. e. macrocarus* Oberholser, 1917 - Andaman Is, Nicobar Is, and islands off W Sumatra (Simeulue, Nias, Batu).  
*C. e. motileyi* Chasen & Kloss, 1929 - NC & W Philippines (Mindoro and Panay to Palawan) and S to Borneo and Java, then E to Sumbawa and Flores.

**Descriptive notes.** 14 cm; male 14-21.5 g, female 14-16 g. Both sexes of nominate race have black spot on forehead, blue and white patch on side of neck, lilac-rufous crown, rump and tail, dark blue back and wings; chin and throat white, rest of underparts pale orange; iris dark brown; bill, legs and feet red. Rufous-backed morph similar, but blue-black areas are rufous to violet-





rufous. Juvenile duller, with less lilac, chin, throat and belly white, bill yellow-orange with pale tip; black-backed morph blue only on scapulars and wing-coverts. Race *motleyi* like nominate but with stronger lilac tones in both forms; *macrocarus* has crown darker, black frontal spot sometimes absent. **VOICE.** High-pitched "tsriet-tsriet" or soft "tjie-tjie-tjie" in flight.

**Habitat.** Deciduous and evergreen primary and secondary forest, alluvial forest, mangroves, overgrown rubber gardens; often seen in thickets of palms, bamboo or shrubs in forest, and often near streams and ponds but also

far from water. Recorded from lowlands up to 1300 m.

**Food and Feeding.** Insects, including mantises (Mantodea), grasshoppers (Orthoptera), flies (Diptera), water beetles (Dytiscidae), winged ants (Formicidae), mayflies (Ephemeroptera); also spiders, worms (Oligochaeta), small crabs, fishes and frogs. Perches low in vegetation or on rocks; flies out to take prey from the ground or from among foliage; takes spiders in their webs or insects in flight; dives into water without submerging for prey at or just below the surface. Once seen flying close to the surface of a stream, and snapping up insects floating downstream. Also enters caves in Sarawak to take insects from the layers of guano. Larger prey are brought back to a perch, where struck repeatedly before being swallowed.

**Breeding.** Lays in Jul-Sept in SW India, in Feb-Jul in Sri Lanka, in Apr-May in NE India, in Mar-Jul in Peninsular Malaysia, in Mar in Sumatra and in Dec-May in Java. Nest in streambank or road cutting, or in terrestrial termitarium, or in soil in roots of a fallen tree, often well away from water; both of pair excavate tunnel 15-100 cm long, 3.8-4.5 cm in diameter, ending in unlined chamber 10-15 cm wide and 5-7 cm high; in sandy soil a pair dug 25 cm of the tunnel in 40 minutes. Clutch 3-7 eggs; no information on incubation and fledging periods.

**Movements.** N populations migrate S to Peninsular Malaysia mainly Aug-Sept, and return N in Mar; large numbers of night-flying migrants reported Aug-Dec at Fraser's Hill and Maxwell's Hill, and even on islands 60 km off W coast, with 65% being immature birds at Fraser's Hill. Ringed birds have returned to same non-breeding grounds in 2 successive seasons. A breeding visitor to many parts of range in India, but its movements there are uncertain.

**Status and Conservation.** Not globally threatened. Widely distributed, but often reported as scarce, particularly in N parts of the range. Apparent scarcity could be a result of its being overlooked, and also a result of its movement patterns. Population levels likely to be reduced as the preferred forest habitat is cleared.

**Bibliography.** Abdulali (1964, 1978), Ali (1969, 1996), Ali & Ripley (1983), Baker (1934a, 1934b), van Balen (1996, 1999), Bangs & Van Tyne (1931), Brown (1979), Burton (1978b), Chasen (1939), Chasen & Hoogerwerf (1941), Coates & Bishop (1997), Daniels (1997), Deignan (1945), Dickinson *et al.* (1991), Duckworth & Kelsch (1988), Duckworth, Salter & Khounboline (1999), Duckworth, Tizard *et al.* (1998), Échécopar & Hùe (1978), Fogden (1976), Grimmett *et al.* (1998), Harrison (1999), Hellebrekers & Hoogerwerf (1967), Henry (1998), Hoffmann (1998), Hoogerwerf (1948b, 1949a, 1949b, 1949c, 1967, 1970), Hoogerwerf & Sicama (1938), Hume (1874), Inskipp, C. & Inskipp (1991), Inskipp, C., Inskipp & Grimmett (1999), Inskipp, T., Lindsey & Duckworth (1996), Jayewardene (1989), Jeyarajasingam & Pearson (1999), Junge (1936), Kennedy *et al.* (2000), Kinnear (1909), Lamfuss (1998), Lekagul & Round (1991), MacKinnon & Philipps (1993, 2000), van Marle & Voous (1988), McClure (1998), Medway & Wells (1976), Meyer de Schauensee (1984), Nash & Nash (1988), Riley (1938), Ripley (1942a), Ripley & Beehler (1987), Robson (2000a), Sims (1959), Smythies (1986, 1999), Stepanyan (1995), Tikader (1984), Vowles & Vowles (1984), Wells (1999), White & Bruce (1986), Wilkinson, Dutton & Sheldon (1991), Zhao Zhengjie (1995).

## 63. Philippine Dwarf-kingfisher

### *Ceyx melanurus*

**French:** Martin-pêcheur flamboyant **German:** Goldfischer **Spanish:** Martin Pigmeo Filipino  
**Other common names:** Philippine Kingfisher/Forest-kingfisher

**Taxonomy.** *Alcedo melanura* Kaup, 1848, Philippines.

Forms a superspecies with *C. erithaca*. Forms *basilanicus* (Basilan) and *platenae* (Mindanao) are synonyms of *mindanensis*; all three described in same year, with precise month of *platenae* disputed, but *mindanensis* generally considered to have priority. Three subspecies recognized.

**Subspecies and Distribution.**

*C. m. melanurus* (Kaup, 1848) - Luzon, Polillo, Alabat and Catanduanes (N Philippines); possibly this race recorded on Tablas.

*C. m. samarensis* Steere, 1890 - Samar and Leyte (C Philippines).

*C. m. mindanensis* Steere, 1890 - Mindanao and Basilan (S Philippines).

**Descriptive notes.** 12 cm. Tiny kingfisher with 3 toes. Both sexes nominate race blue and white neck mark, lilac-rufous head and upperparts, black wings and inner scapulars; chin and throat white, breast and flanks lilac-rufous, belly whitish; iris dark brown; bill, legs and feet red. Juvenile duller, bill orange with pale tip. Race *samarensis* larger, head more lilac, back darker, darker blue spots in wing-coverts, less white on abdomen; *mindanensis* lacks blue neck spot, wings fringed with chestnut. **VOICE.** High-pitched squeak, almost inaudible.

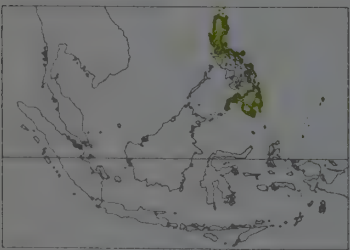
**Habitat.** Dense primary forest, also secondary forest; from coast to 750 m. Often near streams, but these apparently not an essential element of habitat.

**Food and Feeding.** Insects and larvae. Feeding technique not described.

**Breeding.** Specimens with enlarged gonads in May from Samar and in Apr from Luzon. No other information available.

**Movements.** Presumably sedentary.

**Status and Conservation.** **VULNERABLE.** Scarce or rare, but possibly under-recorded owing to its secretive habits. Recent confirmed records from c. 20 sites, mostly on Luzon, but observed also on several other islands. Occurs on Luzon in Quezon National Park, Northern Sierra Madre National Park and Bicol National Park; also recorded in Polillo Watershed Forest Reserve; earlier records also from protected areas on Basilan and Mindanao. Has suffered from extensive de-



struction of forest habitat, including removal of 83% of forest in Sierra Madre Mts since 1930's; continuing clearance of forest is extensive throughout the species' range, and mining and illegal logging are also major threats. Moreover, storms can destroy large areas of forest, as on Catanduanes in 1987 and 1996. More information is urgently needed on its biology and population level.

**Bibliography.** Anon. (1997a), Collar, Crosby & Stattersfield (1994), Collar, Mallari & Tabaranza (1999), Daniels *et al.* (1994), Delacour & Mayr (1946), Dickinson *et al.* (1991), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Gilliard (1950a), Goodman & Gonzales (1990), Inskipp *et al.* (1996), Kennedy *et al.* (2000), Knowles & Nitcher (1995), Mountfort (1988), Parkes (1973), duPont (1971), Poulsen (1995), Ripley & Beehler (1987), Rutgers & Norris (1977), Stattersfield & Capper (2000).

## 64. Sulawesi Dwarf-kingfisher

### *Ceyx fallax*

**French:** Martin-pêcheur multicolore **German:** Rostfischer **Spanish:** Martin Pigmeo de Célebes  
**Other common names:** Celebes/Sulawesi Kingfisher, Celebes Forest Kingfisher, Blue-crowned/Celebes Dwarf-kingfisher, Celebes Pygmy-kingfisher

**Taxonomy.** *Dacelo fallax* Schlegel, 1866, mountainous parts of Sulawesi.

Two subspecies recognized.

**Subspecies and Distribution.**

*C. f. sangirensis* (A. B. Meyer & Wieglesworth, 1898) - Sangihe and Talaud Is.

*C. f. fallax* (Schlegel, 1866) - Sulawesi, and offshore Lembeh I.



**Descriptive notes.** 12 cm. Tiny kingfisher with vestigial fourth toe. Both sexes nominate race black forehead and crown with blue tips, lilac cheeks with white neck spot; dark rufous-brown mantle, scapulars, and wing-coverts, bright blue lower back, rump and uppertail-coverts, black primaries and tail; chin and throat whitish cream, breast dark orange, becoming paler on flanks and belly; iris dark brown; bill, legs and feet red. Juvenile darker and duller, underparts more rufous and lacking violaceous wash, bill black with pale tip. Race *sangirensis* larger, with larger blue markings on crown, and rump more violaceous.

**VOICE.** Thin, repeated, high-pitched "seee".

**Habitat.** Primary lowland and hill forest, sometimes in selectively logged and tall secondary forest; from the coast to 1000 m, mostly below 600 m. Not dependent on water.

**Food and Feeding.** Insects, including grasshoppers (Orthoptera), also small lizards to 11 cm in length. Perches quietly for long periods, low down in the forest, occasionally bobbing head.

**Breeding.** Lays in Nov in Sulawesi. Nest-tunnel in earthen bank, generally away from water. No other information.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Restricted-range species: present in Sulawesi EBA and Sangihe and Talaud EBA. Generally scarce, but perhaps locally somewhat less so in some areas of Sulawesi; recorded from Tangkoko DuaSudara Nature Reserve and in Dumoga-Bone National Park. Possibly extinct on Sangihe I as a result of habitat loss. Extensive destruction of lowland forest throughout its range has probably caused quite considerable reduction in populations of this kingfisher.

**Bibliography.** Andrew (1992), Anon. (1996), van den Berg & Bosman (1986), Catterall (1997), Coates & Bishop (1997), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Holmes & Philipps (1996), Inskipp *et al.* (1996), Jepson (1997), Knowles & Nitcher (1995), Riley (1997a), Ripley & Beehler (1987), Rozendaal & Dekker (1989), Sampiri (1996), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Stresemann (1940), Sujatnika *et al.* (1995), Wardill (1995), Wardill *et al.* (1999), Watling (1983), White & Bruce (1986).

## 65. Madagascar Pygmy-kingfisher

### *Ceyx madagascariensis*

**French:** Martin-pêcheur malgache **Spanish:** Martin Pigmeo Malgache  
**German:** Madagaskarzwergfischer

**Other common names:** Madagascar Rufous Kingfisher

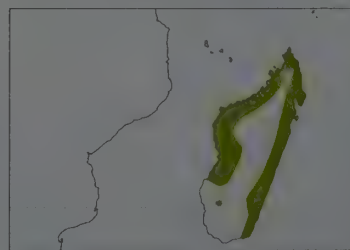
**Taxonomy.** *Alcedo madagascariensis* Linnaeus, 1766, Madagascar.

Sometimes placed in *Corythornis* or *Ispidina*, but appears to be more closely related to Oriental *Ceyx* species than to African ones. Race *dilutus* often misspelt *diliutus*. Two subspecies recognized.

**Subspecies and Distribution.**

*C. m. madagascariensis* (Linnaeus, 1766) - Madagascar except SW.

*C. m. dilutus* (Benson, 1974) - Sakaraha, in arid SW of Madagascar.



**Descriptive notes.** 13 cm; male 17-21 g, female 17-22 g. Both sexes nominate race bright rufous above, washed with lilac on lower back to uppertail-coverts, and on rear half of head; white neck spot, black primaries; white below, sides and flanks rufous; iris dark brown; bill, legs and feet orange-red. Juvenile duller, reduced lilac wash, bill black with pale tip. Race *dilutus* paler, and lacks lilac wash. **VOICE.** High-pitched squeak; "treet treet"; when disturbed, gives high, harsh "chweip" or "treeeee" as it flies off.

**Habitat.** Dry scrub, savanna woodland, and margins and interior of wet evergreen forest;

from the coast up to c. 1500 m. Not dependent on water.

**Food and Feeding.** Mainly frogs; also insects, including grasshoppers (Orthoptera), beetles (Coleoptera), earwigs (Dermaptera), ants (Formicidae), and larvae; also spiders, shrimps, and small lizards (Uroplattidae) and chameleons (Chamaeleonidae). Sits on a low branch in dense undergrowth, watching for prey; darts down to snatch it from the ground and returns to perch, where prey bashed against branch before being swallowed.



**Breeding.** Lays in Oct-Jan, mainly Nov-Dec. Nest-tunnel 30-35 cm long, 5 cm in diameter, excavated in earth bank, often at edge of forest trail. Clutch 4 eggs; both sexes incubate; no information on incubation and fledging periods.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Nominate race is fairly common and widely distributed in E, N & NW of island. Race *dilutus* is rare, known from only a single specimen collected in 1970's in the Sakaraha Forest, in arid SW of the island; further field searches desirable to confirm that it still survives in this area, which is little visited by ornithologists.

**Bibliography.** Benson (1974), Benson *et al.* (1976-1977), Dee (1986), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Forshaw & Cooper (1983, 1985), Fry (1980a), Fry *et al.* (1992), Knowles & Nitehen (1995), Langrand (1994, 1995a, 1995c), Milon *et al.* (1973), Morris & Hawkins (1998), Ramanitra (1995), Rand (1936), Safford & Duckworth (1990), Sinclair & Langrand (1998), van Someren (1947), Steinbacher (1972), Thorstrom & Watson (1997), Young (1995).

## 66. Variable Dwarf-kingfisher

### *Ceyx lepidus*

**French:** Martin-pêcheur gracieux **German:** Waldfischer **Spanish:** Martín Pescador Variable  
**Other common names:** Dwarf/Gentian Kingfisher, Variable Kingfisher, Dwarf/Variable Forest-kingfisher, Goodfellow's Kingfisher (*margarethae*)

**Taxonomy.** *Ceyx lepidus* Temminck, 1836, Ambon.

Shows similarities in plumage to species of *Alcedo*, and has often been allocated to that genus, but feeding ecology much closer to that of other *Ceyx* species. Philippine form that was formerly considered a full species, "*Ceyx goodfellowi*", subsequently shown to be variant of the race *margarethae* of present species. Birds of Buka and Bougainville have sometimes been separated as race *pallidus*, but now considered more appropriately lumped into *meeki*. Fourteen subspecies currently recognized.

**Subspecies and Distribution.**

*C. l. margarethae* A. W. H. Blasius, 1890 - Banton, Tablas, Romblon, Sibuyan, Semirara, Negros, Cebu, Olango, Siquijor, Camiguin Sur, Mindanao, Basilan, Malamaui, Jolo, Tawitawi and Bongao (C & S Philippines).

*C. l. uropygialis* G. R. Gray, 1860 - Morotai, Halmahera and Ternate, Tidore, Bacan, Bisa and Obi (N Moluccas).

*C. l. wallacii* Sharpe, 1868 - Sula Is (Soho, Taliabu, Mangole, Sanana).

*C. l. cajeli* Wallace, 1863 - Buru (S Moluccas).

*C. l. lepidus* Temminck, 1836 - Ambelau, Ambon, Seram, Saparua, Seram Laut and Watubela (S Moluccas).

*C. l. solitarius* Temminck, 1836 - W Papuan Is, islands in Geelvink Bay, Aru Is, and mainland New Guinea E (including Kairiru I and Karkar I) to D'Entrecasteaux Is.

*C. l. dispar* Rothschild & Hartert, 1914 - Manus I in Admiralty Is (NW Bismarck Archipelago).

*C. l. mulcatus* Rothschild & Hartert, 1914 - New Hanover, New Ireland, Tabar Is and Lihir Is.

*C. l. sacerdotis* E. P. Ramsay, 1882 - New Britain, and nearby islands of Umboi, Lolobau and Watom.

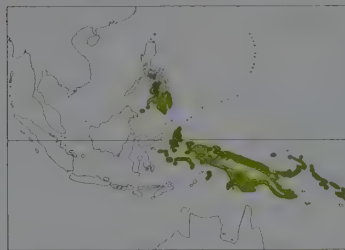
*C. l. meeki* Rothschild, 1901 - Buka and Bougainville E to Choiseul and Santa Isabel (W & C Solomons).

*C. l. collectoris* Rothschild & Hartert, 1901 - New Georgia Group (WC Solomons).

*C. l. nigromaxilla* Rothschild & Hartert, 1905 - Guadalcanal (E Solomons).

*C. l. malaitae* Mayr, 1935 - Malaita (E Solomons).

*C. l. gentianus* Tristram, 1879 - San Cristobal (E Solomons).



**Descriptive notes.** 14 cm; male 11-21 g, female 13-24 g. Small kingfisher with 3 toes. Both sexes of nominate race have orange loreal spot, white bar on side of neck, blackish head and wings spotted with dark blue, brilliant ultramarine-blue back, silvery-blue rump; buffy-white chin and throat, rest of underparts rich orange; bill red; iris dark brown; legs and feet orange to orange-yellow. Juvenile darker above, less blue, bill orange with dusky base and pale tip. Races vary considerably in plumage coloration, and in bill shape and colour: underparts rufous or buffy in most; some have bill dorsoventrally flattened and red, typical of

genus, others have bill laterally flattened and black, more like *Alcedo*; *margarethae* dimorphic, pale morph pale blue above; *cajeli* has black head and wings contrasting with silvery-blue back and rump; *solitarius*, *mulcatus*, *meeki* and *gentianus* have black bill, last also pure white underparts; *nigromaxilla* has upper mandible mainly black, lower mainly orange-red; *sacerdotis* has upper mandible dusky; *dispar* sexually dimorphic, male has blackish head spotted with blue, female largely orange head with dark blue restricted to stripe on hindcrown. VOICE. Shrii repeated "tzeep" in flight, also shrii "chree"; possible duetting by paired birds.

**Habitat.** Primary and secondary rainforest, monsoon forest, thick vegetation along streams, overgrown plantations; from the coast up to 1300 m. Usually found in middle levels of forest, at 0-25 m; although frequently found along streams, is not dependent on water.

**Food and Feeding.** Insects, such as dragonflies (Odonata), mayflies (Ephemeroptera), midges (Culicomorpha), grasshoppers and locusts (Orthoptera), crickets (Grylloidea); also spiders, and small frogs and tadpoles. Sits on a low branch, rock, fallen tree trunk or stump, occasionally bobbing head and flicking tail, searching for prey; some prey are taken in air, in swift, direct flight over water or in forest; others taken on ground away from water.

**Breeding.** Lays in Nov-Jan in New Guinea, in Jul-Sept in New Britain and on Bougainville, in Sept in Moluccas. Nest in an earth or streamside bank, in earth around roots of a fallen tree, or in termite nest; short tunnel, 5-7.5 cm in diameter, with nest-chamber at end. Clutch 2 eggs; no information on incubation and fledging periods.

**Movements.** Sedentary; in SE New Guinea, an individual of *solitarius* was retrapped over 6 years later at the same site, but recapture rate was generally very low, suggesting either high mortality or a non-sedentary population.

**Status and Conservation.** Not globally threatened. Species is widely distributed, over a great number of islands, and is common in many areas. Density in New Guinea 1 bird/10 ha. Some subspecies, however, have a much more restricted range, and could be threatened by habitat loss.

**Bibliography.** Andrew (1992, 1993), Beehler (1978), Beehler *et al.* (1986), Cam & Galbraith (1956), Coates (1985), Coues & Bishop (1997), Davidson *et al.* (1995), Delacour & Mayr (1946), Diamond (1972), Diamond & LeCroy (1979), Dickinson *et al.* (1991), Doughty *et al.* (1999), Evans, Dutton & Brooks (1993), Evans, Magsalay *et al.* (1993), Finch (1980a), Gilliard & LeCroy (1967a), Greenway (1966), Gregory (1995a), Hadden (1981), Hartert (1903), Inskipp *et al.* (1996), Isherwood *et al.* (1997), Kennedy *et al.* (2000), Mackay (1980), Mayr (1945), Mayr & Rand (1937), McGregor (1906), Mees (1965), Pearson (1975b), Peekover & Filewood (1976), Pfeiffer (1963), duPont (1971), duPont & Rabor (1973a), Rand (1942a, 1942b), Rand & Gilliard (1967), Ripley (1964), Ripley & Rabor (1958), Schodde (1977), Schönwetter (1966), Stones *et al.* (1997), Webb (1992), White & Bruce (1986), Wollaston (1912).

*ssp bowdleri*

68

*ssp leucogaster*

67

*ssp leopoldi*

*ssp galerita*

*ssp johannae*

*ssp cristata*

70

71

*ssp vintsioides*

69

*ssp flumenicola*

72

*ssp argentata*

*ssp cyanopectus*

73

*ssp nigrirostris*

*ssp euryzona*

74

75

*ssp peninsulae*

PLATE 18

inches

3

cm

8



# Genus *ALCEDO* Linnaeus, 1758

## 67. White-bellied Kingfisher

### *Alcedo leucogaster*

**French:** Martin-pêcheur à ventre blanc **Spanish:** Martín Pescador Ventriblanco  
**German:** Weißbauch-Zwergfischer

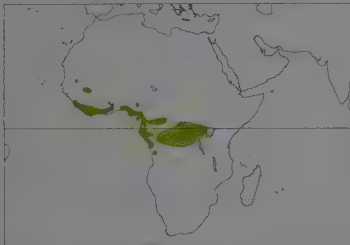
**Taxonomy.** *Halcyon leucogaster* Fraser, 1843, Clarence, Bioko (Fernando Póo). Closely related to *A. cristata* and *A. vintsioides*, and sometimes placed with them in a separate genus *Corythornis*; closely related also to *A. nais* and *A. thomensis*, either or both of which have often been treated as conspecific with present species. Population from S Nigeria to N Angola formerly separated as race *batesi*, but appears indistinguishable from nominate. Three subspecies currently recognized.

#### Subspecies and Distribution.

*A. l. bowdleri* Neumann, 1908 - S Mauritania (Guidimaka), SW Mali (Mandingo Mts), and Guinea to S Ghana.

*A. l. leucogaster* (Fraser, 1843) - SW Nigeria to S Cameroon, Bioko I (Fernando Póo), Gabon and NW Angola.

*A. l. leopoldi* (Dubois, 1905) - Congo Basin in S Central African Republic and from Zaire E to S Uganda (Sango Bay, Mabira Forest).



**Descriptive notes.** 13 cm; male 14-15 g, female 14-17 g. Both sexes nominate race chestnut cheeks and ear-coverts, white stripe on side of neck, eyestripe rufous with lilac tinge; crown and wings blue-black, barred with ultramarine-blue; hindneck, back and tail ultramarine, more brilliant on rump; white below, chestnut breast side and flank; bill orange-red, darker on culmen; iris dark brown; legs and feet red. Juvenile black bill, blue mottling on mantle, more barring on crown, speckled moustache. Race *bowdleri* broader rufous stripe above eye; *leopoldi* paler, chestnut breast sides unite forming breastband, crown

greenish-blue and black, superciliary area blue. **VOICE.** Not recorded.

**Habitat.** Dense primary and secondary forest, gallery forest, dense thickets along streams, wooded and mangrove swamps, tidal estuaries, open undergrowth in dry forest, *Marquesia* thickets, also gardens, ponds and cocoa plantations; often along small streams or marshes. From sea-level to 1200 m; to 1800 m on Bioko.

**Food and Feeding.** Feeds equally on fish and insects; insects include dragonflies and damselflies (Odonata), aquatic insect larvae, cockroaches (Blattoidea), beetles (Coleoptera), winged termites (Isoptera), ants (Formicidae), wasps (Hymenoptera). Also takes spiders, earthworms (Oligochaeta), frogs, tadpoles, and lizards. Watches quietly from a low branch, usually near a forest stream, bobbing head and flicking tail; prey taken from the ground or in water.

**Breeding.** Lays in Jul and Oct in Cameroon, in Dec or possibly earlier in Gabon. Nest in a streamside bank or in sloping ground. Clutch 2 eggs; no information on incubation and fledging periods.

**Movements.** Probably mainly sedentary. Vagrants recorded in NW Zambia and N Nigeria suggest that some birds wander, probably moving at night; the one in N Nigeria was caught alive at dawn in a second-storey room, over 600 km N of its normal range, following a night of severe wind and rainstorms driving N.

**Status and Conservation.** Not globally threatened. Has a wide distribution in several habitats. Although generally uncommon, this species is often overlooked; it has been found to be locally common in some areas, as in Gabon, SW Mali and W Uganda.

**Bibliography.** Allport *et al.* (1989), Amadon (1953), Anon. (1995b), Aspinwall & Beel (1998), Bannerman (1953), Benson *et al.* (1971), Bouet (1961), Button (1967), Cheke & Walsh (1996), Clancey (1978c, 1992), Colston & Curry-Lindahl (1986), Dean (2000), Dekeyser & Derivot (1966), Deme & Fishpool (1994), Dowsett (1989b), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Dowsett-Lemaire & Dowsett (1999, 2000), Elgood *et al.* (1994), Field (1999), Friedmann (1969, 1978), Friedmann & Williams (1969), Fry (1967c, 1967d, 1980a), Fry & de Naurois (1984), Fry *et al.* (1988), Gartshore (1989), Gartshore *et al.* (1995), Gatter (1988, 1997), Gee & Heigham (1977), Grimes (1987), Hamel (1980), Heigham (1976), Hockey (1997), Lippens & Wille (1976), Loeuffe (1981b), Mackworth-Praed & Grant (1962, 1970), Pérez del Val (1996), Pérez del Val *et al.* (1994), Pinto (1983), Sargeant (1993), Serle (1981), Short *et al.* (1990), Snow (1978), Thiollay (1973a), Traylor (1963), Wells (1968).

## 68. Principe Kingfisher

### *Alcedo nais*

**French:** Martin-pêcheur de Principé **Spanish:** Martín Pescador de Principe  
**German:** Principezwergfischer

**Taxonomy.** *Alcedo Nais* Kaup 1848, Principe.

Has been regarded as conspecific with either *A. leucogaster* or *A. cristata*; seems closer to former in habits and habitat, but more similar to latter in certain aspects of its plumage; given complete uncertainty as to whether it is actually closer to one or the other, probably best tentatively regarded as a distinct species, though further study needed to clarify this. Monotypic.

**Distribution.** Principe, in Gulf of Guinea.

**Descriptive notes.** 13 cm; 15 g. Both sexes chestnut lores, ear-coverts and neck side, white neck blaze; crown and upperparts ultramarine-blue, crown with black bands; chin and throat white, underparts rufous, darker on breast, paler in centre of abdomen; bill red; iris dark brown; legs and feet red. Differs from very similar *A. leucogaster* in having paler crest more distinctly banded, no rufous above eye, more rufous on underparts. Juvenile crown and malar region more barred with black,



dusky breast, black bill with white tip. **VOICE.** Short "tsip" and, on take-off, disyllabic "tsi-vit"; "tsiirirri tieup tieup" during courtship.

**Habitat.** Aquatic habitats on Principe somewhat limited, so found more frequently in open areas, far from water, than is *A. thomensis*. Frequently seen in secondary forest and woodland, along roads, in plantations and gardens, often far from water, but also found along streams and at small ponds, and on coastal beaches. Diversity of habitats occupied contrasts with ecological exigencies of *A. leucogaster* in C Africa, which inhabits only

streams and small rivers in forested environments.

**Food and Feeding.** Mainly insects, such as cockroaches (Blattoidea) and grasshoppers (Orthoptera); also small fish; also spiders, earthworms (Oligochaeta); food remains found in a nest included lizard bones, beetles (Coleoptera), wasps (Hymenoptera), damselflies (Zygoptera), and crabs. Hunting perches include rocks in rivers, as well as large bankside trees, banana trees in plantations, bushes, and electricity wires, up to c. 20 m above ground but usually lower. Flies down to take prey from ground or from surface of a stream, returning with it to its perch, where prey may be hit against perch before being swallowed.

**Breeding.** Lays in Sept-Feb, juvenile being fed by adult end Jan. In courtship, mutual chasing while calling, with constant changes of perch, also perching side by side with jerky greeting movements interspersed with tail-flicking. Nest in bank of a stream, at side of track or path or on slope or crest of ridge. No other information.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in Principe EBA. Although very restricted in distribution, it is widespread throughout Principe, and reported to be common in low-lying country. Common along R Papagaio, from mouth of river up to central valley. Biology poorly known, and requires investigation.

**Bibliography.** Amadon (1953), Atkinson *et al.* (1994), Bannerman (1953), Christy & Clarke (1998), Clancey (1992), Forshaw & Cooper (1983, 1985), Fry (1980a), Fry & de Naurois (1984), Fry, Fry & Harris (1992), Fry, Keith & Urban (1988), Hockey (1997), Jones & Tye (1988), Knowles & Ntchen (1995), Mackworth-Praed & Grant (1970), de Naurois (1994), Sargeant (1992, 1994), Snow (1950), Stattersfield *et al.* (1998).

## 69. Sao Tome Kingfisher

### *Alcedo thomensis*

**French:** Martin-pêcheur de Sao Tomé **Spanish:** Martín Pescador de Santo Tomé  
**German:** Sao-Tomé-Zwergfischer

**Taxonomy.** *Corythornis thomensis* Salvadori, 1902, São Tomé.

Has often been considered a race of *A. leucogaster* or of *A. cristata*; seems close to latter in habits, habitat and adult plumage, but its geographical isolation and very distinctive immature plumage suggest that it is better treated as a distinct species; further research needed. Monotypic.

**Distribution.** São Tomé, in Gulf of Guinea.



**Descriptive notes.** 14 cm; 20 g. Both sexes have black crown and crest with greenish-blue margins and bars, rich ultramarine-blue mantle, back and rump; white neck blaze, rufous ear-coverts, cheeks and side of breast, malar area with dusky marks, white chin and throat, cinnamon-rufous underparts; bill coral-red; iris dark brown; legs and feet orange-red. Differs from very similar *A. cristata* in shorter crest feathers with less obvious banding, darker rufous cheeks, darker purple-blue rump. Juvenile much duller, with general dusky black plumage, crest more greenish, mantle and back black with blue wash and margins, giving spangled

appearance, loreal spot white, breast dusky black, belly buff, becoming rufous on undertail-coverts, bill black. **VOICE.** Clear rattling calls during mutual chasing, but courtship calls insufficiently described.

**Habitat.** Generally near water, on highland streams, rivers in town, streams in coconut plantations, and along seashore; sea-level to 1250 m. Found at mouths of all rivers on island, also along river valleys, including in cultivated regions and areas of bamboo; common on torrent-like upland streams in SW of island. Also lagoons and mangroves, and more open swamps; more rarely, in open areas at roadsides and borders of plantations. In general, however, occupies less open habitats than *A. cristata*, notably the banks of forest streams and rivers, where *A. cristata* never found in Africa.

**Food and Feeding.** Little known; insects and fish recorded. Probably similar to *A. cristata*. Fishes from streamside rocks or from shingle in riverbed; in open swamps, hunts from low branch or tree roots; also seen chasing insects from perch on electricity wires, a habit which, in C Africa, is more typical of *Ceyx pictus* than of *A. cristata*.

**Breeding.** Young with adults seen end Dec and beginning Jan, end Mar/early Apr, and end Aug; nest with young early Apr; immature collected in Jan. Nest in streambank, or in earth bank not more than 60 m from a stream. No other information.

**Movements.** Presumed to be sedentary.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in São Tomé EBA. Although very restricted in distribution, it is reported to be common on island of São Tomé, where it occupies all favourable habitats; absent only from mountainous central massif and from forest undergrowth. Information required on its ecology and biology.

**Bibliography.** Amadon (1953), Atkinson *et al.* (1994), Bannerman (1953), Christy & Clarke (1998), Clancey (1992), Forshaw & Cooper (1983, 1985), Fry (1980a), Fry & de Naurois (1984), Fry, Fry & Harris (1992), Fry, Keith & Urban (1988), Jones & Tye (1988), Knowles & Ntchen (1995), Mackworth-Praed & Grant (1970), de Naurois (1994), Sargeant (1992, 1994), Snow (1950), Stattersfield *et al.* (1998).



## 70. Malachite Kingfisher

*Alcedo cristata*

French: Martin-pêcheur huppé

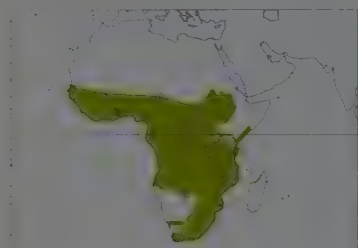
German: Haubenzwergfischer

Spanish: Martín Pescador Malaquita

Other common names: Diademed Kingfisher(!)

**Taxonomy.** *Alcedo cristata* Pallas, 1764, Cape of Good Hope.

Closely related to *A. leucogaster* and *A. vintsioides*, and sometimes placed with them in a separate genus *Corythornis*; forms a superspecies with *A. vintsioides*; also close to *A. nais* and *A. thomensis*, with both of which it has been regarded as conspecific. Racial divisions confused, and further work needed for clarification; recent works have listed three or four races, but with very divergent distributions for some of them; proposed forms *robertsi* and *cyanostigma* are synonyms of nominate. Three subspecies currently recognized.

**Subspecies and Distribution.***A. c. galerita* P. L. S. Müller, 1776 - Senegal E to Ghana.*A. c. cristata* Pallas, 1764 - Nigeria E to Sudan, Uganda and Kenya, and S to S Angola, N Namibia and Botswana, Zimbabwe and South Africa.*A. c. stuartkeithi* (Dickerman, 1989) - Sudan (Blue Nile), Ethiopia and S Somalia; possibly resident also in E. Yemen (2 records).

**Descriptive notes.** 13 cm; 12-19 g. Both sexes of nominate race have rufous supraloral spot, long forehead and crown feathers forming crest banded with black and pale greenish-blue; white neckstripe; hindneck and upperparts glossy ultramarine-blue; chin and throat white, cheeks, breast and flanks orange-rufous, belly buff; iris dark brown; bill, legs and feet red. Juvenile duller, dusker, bill black. Race *galerita* deeper orange-rufous underparts; *stuartkeithi* also deeper orange below, paler rump and vent. **Voice.** Short, shrill, repeated "seek, seek"; song, used in duet, "ii-tiii-cha-cha, chui chui tuichui chui", ending with a

chuckle.

**Habitat.** Fresh waters, including marshes, dams, ponds, lakes, slow-flowing rivers, streams, tidal estuaries, mangroves, gravel pits, sewage ponds, and irrigation canals with fringing reeds and rank vegetation. During breeding season more often associated with small watercourses, probably owing to requirement of banks for nesting.

**Food and Feeding.** Mainly aquatic animals, including small prawns and crabs, tadpoles and small frogs and fish, also water beetles (Dytiscidae), water boatmen (Notonectidae), and insect larvae (e.g. of Odonata); some prey taken from land, such as mantises (Mantodea), beetles (Coleoptera), grasshoppers (Orthoptera) and lizards. At L Naivasha, in Kenya, birds each ate 15-20 small *Tilapia grahami* fish per day; this number doubled when they were breeding, with an additional 60-70 fish fed daily to 5 nestlings. Perches low over the water, often on a reed, searching for prey, occasionally bobbing head and flicking tail, crest being raised and lowered; then dives steeply into water with a small splash, returns with prey in its bill to perch, where prey beaten until still and then swallowed. At L Nakuru, in Kenya, fished from perches 20-50 cm above the water, and spent most time in areas with high fish density; seemed to avoid areas with dense vegetation, and had less success there. Foraging behaviour at L Victoria did not change after the introduction of Nile perch (*Lates niloticus*), and it continued to hunt within a few metres of the shore. When fish were killed by pollution in a stream in S Kenya, the birds remained and fed on water beetles and water boatmen, caught on the surface, and dragonflies, caught in flight.

**Breeding.** Lays in Apr-Dec in W Africa; in Jun-Oct in C Africa; in Mar, May, Jul, Oct and Nov in Uganda; in Apr-May, Jul, Oct and Dec in S Kenya and E Tanzania; in all months, mainly Feb-Mar and Jun-Sept, in Zambia; in Sept-Jun in Malawi and S Mozambique; and in Aug-Feb, mainly Sept-Oct, but can extend to May, in Zimbabwe and South Africa; at L Nakuru (Kenya) breeding coincided with periods of high fish density, and in Okavango Basin (N Botswana) is in May-Oct just after peak of floods; 3 or 4 broods can be reared in a season. Several pairs may nest together, but generally is strongly territorial. Nest-site a streamside bank, road cutting, pit, earth mound, soil in roots of a fallen tree, or below ground in side of an aardvark (*Oryzomys afer*) burrow, and an exceptional report of a nest 4 m down a well shaft; tunnel dug by both of pair, 25-125 cm long, straight or curved, and inclined; several tunnels may be started but only one completed; nest-chamber lined with fish bones and regurgitated arthropod exoskeletons. Clutch 3-6 eggs, mean 3-8 in South Africa; incubation period 14-16 days; both sexes brood chicks, which remained in a nest for at least 15 days. A pair reared 9 young from 3 broods in 4 months in Kenya; a captive pair in Malawi, only 6 months old, raised 14 young from 4 broods in 4-5 months.

**Movements.** Sedentary at some locations, e.g. L Naivasha, but at least partially migratory or nomadic elsewhere. Present only Dec-Mar at M'Passa, in Gabon, and more common in Jun-Nov in N Nigeria; in S Malawi, adults are sedentary but juveniles disperse widely; in Zimbabwe and South Africa dispersal occurs during austral summer wet season into otherwise dry country, particularly on the plateau, and then a return to coast (e.g. at Natal) at the start of the dry season. Dispersing juveniles may fly at night. Possible long-distance migration suggested by 2 records in N Somalia, in Dec and Apr, which could also be linked with the 2 recent records of this species in Yemen.

**Status and Conservation.** Not globally threatened. Widespread and often common, even locally abundant at times, throughout range; becomes less common at higher latitudes and altitudes. Density of 8 birds/km along L Naivasha's shoreline. No threats evident; dispersing juveniles are sometimes killed at night by flying into windows, mainly during May-Aug, in South Africa.

**Bibliography.** Ash (1994), Ash & Miskell (1983, 1998), Bannerman (1953), Barlow *et al.* (1997), Benson & Benson (1977), Benson *et al.* (1971), Birkenmeier (1969), Bouet (1961), Brunel (1958), Cave & Macdonald (1955), Chapin (1939), Cheke & Walsh (1996), Christy & Clarke (1994), Clancey (1964a, 1965a, 1971a, 1978a, 1990, 1992, 1996), Curry-Lindahl (1960), Dean (1971, 1974, 2000), Dekeyser & Derivot (1966), Dickerman (1989), Dowsett (1971b), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Elgood *et al.* (1994), Evans, M.I. (1994), Farrow (1994), Field (1999), Fry (1965, 1980a), Fry & de Naurois (1984), Fry *et al.* (1988), Garrett (1996), Gatter (1997), Gee & Heigham (1977), Germain *et al.* (1973), Ginn *et al.* (1989), Girardoux *et al.* (1988), Glover *et al.* (1970), Greig-Smith (1976), Grimes (1987), Hammer (1976, 1980b), Harrison *et al.* (1997), Harwin (1984a), Hockey (1997), Hockey *et al.* (1989), Hollom *et al.* (1988), Jackson (1972), Jennings (1995), Kemp (1974), Kirwan (1993), Lewis & Pomeroy (1989), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Meadows (1977), Newman (1974), Pakenham (1979), Parker (1999), Penny (1994), Pinto (1983), Poncer *et al.* (1996), Reyer *et al.* (1988), Rodwell *et al.* (1996), Rutgers & Norris (1977), Salomonsen (1934), Serle *et al.* (1977), Short *et al.* (1990), Snow (1978), van Someren (1956), Steyn (1984), Tomlinson (2000), Tucker (1981), Wanink (1996), Wilson, J. (1993), Zimmerman *et al.* (1996).

## 71. Madagascar Kingfisher

*Alcedo vintsioides*

French: Martin-pêcheur vintsi

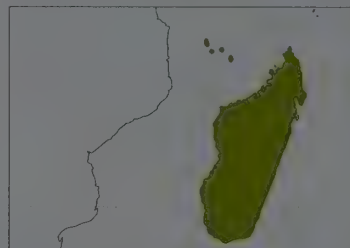
German: Madagaskarzwergfischer

Spanish: Martín Pescador Malgache

Other common names: Diademed(!)/Malagasy Kingfisher, Madagascar Malachite Kingfisher

**Taxonomy.** *Alcedo Vintsioides* Eyndoux and Gervais, 1836, Madagascar.

Closely related to *A. leucogaster* and *A. cristata*, and sometimes placed with them in a separate genus *Corythornis*; forms a superspecies with *A. cristata*. Two subspecies recognized.

**Subspecies and Distribution.***A. v. johannae* (Meinertzhagen, 1924) - Comoro Is.*A. v. vintsioides* Eyndoux & Gervais, 1836 - Madagascar.

**Descriptive notes.** 13 cm; male 16-21 g, female 18-22 g. Both sexes nominate race forehead and crown pale green-blue and banded with black; mantle, wings and tail deep ultramarine, back and rump paler azure-blue; throat and neck patch white, cheeks and underparts rufous, paler on belly; bill black with dull red base; iris dark brown; legs and feet orange-red. Juvenile duller, upperparts with black wash, breast and belly buff. Race *johannae* paler, more green-blue. **Voice.** Shrill high-pitched "seek", repeated rapidly in flight, or very shrill "treeeeee" on taking flight.

**Habitat.** Rivers, streams, lakes, swamps, estuaries, mangroves, coast and tidal pools; also paddyfields and coconut plantations, usually with fringing trees or reeds, and into forest; sometimes far from fresh water, e.g. in coastal scrub in arid SW Madagascar. From sea-level to 1800 m. On volcanic Grand Comoro, found on the coast and at crater lakes.

**Food and Feeding.** Small fish, frogs, marine and freshwater crustaceans, also aquatic and terrestrial insects, e.g. grasshoppers (Orthoptera), bugs (Hemiptera), flies (Diptera) and beetles (Coleoptera). Sits on a low perch, searching for prey; dives into water or snatches prey from ground, then returns to perch with its prey, which is repeatedly beaten before being swallowed. On Grand Comoro, a bird sat on rocks exposed by the low tide and repeatedly flew 10 m to a cliff to catch small crabs hiding in the cracks, then returned to its perch to eat them.

**Breeding.** Lays in Sept-Apr in Madagascar and in Oct in Comoros. Both sexes excavate a tunnel 5 cm wide and 40 cm long, with nest-chamber at end, in a streamside bank or in an earth bank which can be up to 200 m from water. Clutch 3-6 eggs; both sexes incubate, and both care for young; incubation and fledging periods not recorded.

**Movements.** Probably sedentary.

**Status and Conservation.** Not globally threatened. Widely distributed and fairly common in Madagascar, occurring in a range of habitats. No apparent threats, and is present in several protected areas, as Ranomafana National Park and Perinet Special Reserve in Madagascar. No detailed data from Comoros, but thought to be reasonably common there.

**Bibliography.** Appert (1996), Benson (1960), Benson *et al.* (1976-1977), Clancey (1992), Collin & Collin (1996), Dee (1986), Forbes-Watson (1969), Forshaw & Cooper (1983, 1985), Fry (1980a), Fry & de Naurois (1984), Fry *et al.* (1992), Knowles & Nitcher (1995), Langrand (1995a), Louette (1988a), Louette & Schoeters (1983, 1984), Milon *et al.* (1973), Morris & Hawkins (1998), Ramanitra (1995), Rand (1936), Sinclair & Langrand (1998), van Someren (1947), Thompson *et al.* (1987), Thorstrom & Watson (1997), Tingay & Gilbert (1999), Young (1995).

## 72. Silvery Kingfisher

*Alcedo argentata*

French: Martin-pêcheur argenté

German: Silberfischer

Spanish: Martín Pescador Plateado

**Taxonomy.** *Ceyx argentata* Tweeddale, 1877, Dinagat, Philippines.

Sometimes placed in the genus *Ceyx*. Forms a superspecies with *A. cyanopectus*. Two subspecies recognized.

**Subspecies and Distribution.***A. a. flumenicola* (Steere, 1890) - Samar, Leyte and Bohol (SC Philippines).*A. a. argentata* (Tweeddale, 1877) - Dinagat, Siargao, Mindanao and Basilan (S Philippines).

**Descriptive notes.** 14 cm. Distinctive small kingfisher with pied plumage. Both sexes nominate race black head with white or blue-white frontal spot, neck patch, mottling on side of crown; black scapulars, wings and tail, white spots on median wing-coverts, white back, rump and uppertail-coverts with pale azure-blue tips; white throat, blue-black breast, white belly; bill black; iris dark brown; legs and feet orange-red. Juvenile pale rufous frontal spot and neck patch, creamy-buff chin to upper breast. Race *flumenicola* smaller, purplish flanks and breast, creamy throat, frontal spot and neck patch. **Voice.** Soft, high-pitched

"wheet", given in flight.

**Habitat.** Primary or secondary rainforest having streams, small rivers and pools with well-timbered banks and dense overhanging growth; may tolerate selectively logged forest with similar habitat elements, or wooded streams in coconut plantations near forest edge. Mainly below 1000 m.

**Food and Feeding.** Small fish and crabs. Perches on a low branch of streamside shrub or rock, and dives in to catch prey, returning with it to perch.

**Breeding.** Female with enlarged ovary in May, and juveniles collected in Apr-May. Evidently nests in streamside bank. No other information available.

**Movements.** Presumably sedentary.

**Status and Conservation.** VULNERABLE. Restricted-range species; present in Mindanao and the Eastern Visayas EBA. Generally rare; recorded from c. 10 sites since 1980, in Leyte, Bohol and E Mindanao; inconspicuous and shy, however, and possibly under-recorded. Formerly locally common and widespread; has suffered rapid decline as a result of loss and degradation of lowland



forest with clear streams and pools. Continuing clearance of lowland forest, combined with pollution of streams, likely to depress population even further. Occurs in Rajah Sikatuna National Park on Bohol, and at Agusan Marsh Protected Area on Mindanao; at former site, habitat threatened by soil erosion, agricultural expansion and cutting of trees. Forest at Bislig, on Mindanao, also an important site for this species, but being cleared for replanting with exotics. More information on its biology and status is urgently required.

**Bibliography.** Anon. (1997a), Collar, Crosby & Stattersfield (1994), Collar, Mallari & Tabaranza (1999), Delacour & Mayr (1946), Dickinson *et al.* (1991), Evans, Dutton & Brooks (1993), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Hachisuka (1933), Inskipp *et al.* (1996), Kennedy *et al.* (2000), Knowles & Nitehen (1995), duPont (1971), duPont & Rabor (1973b), Rand & Rabor (1960), Robson (1997, 1999b), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Tomlinson (2000).

## 73. Indigo-banded Kingfisher

### *Alcedo cyanopectus*

**French:** Martin-pêcheur à poitrine bleue **Spanish:** Martin Pescador Pechiazul  
**German:** Blaubrutfischer

**Other common names:** Blue-breasted/Dwarf River/Philippine Pectoral Kingfisher

**Taxonomy.** *Ceyx cyano-pectus* Lafresnaye, 1840, Luzon.

Sometimes placed in the genus *Ceyx*. Forms a superspecies with *A. argentata*. Two subspecies recognized.

**Subspecies and Distribution.**

*A. c. cyanopectus* (Lafresnaye, 1840) - Luzon, Polillo, Catanduanes, Mindoro, Marinduque, Sibuyan, Masbate and Ticao (N Philippines).

*A. c. nigrirostris* (Bourne & Worcester, 1894) - Panay, Negros and Cebu (C Philippines).



**Descriptive notes.** 13 cm. Male of nominate race has crown, cheeks and hindneck black with ultramarine tips; rufous frontal spot, white neck patch rufous at rear; scapulars, wings and tail blackish with blue wash, wing-coverts tipped with bright blue, mantle, back, rump and uppertail-coverts brilliant blue; chin white, throat pale rufous, becoming darker rufous on breast and belly; breast crossed by two cobalt-blue bands, thinner in centre and extending to flanks; upper mandible greyish-black, most of lower mandible red; iris dark brown; legs and feet red. Female single pectoral band, often broken in middle. Juvenile orange-rufous underparts with purple-blue patch at side of breast. Race *nigrirostris* black bill, single breastband, incomplete on female, paler and more spangled upperparts, deeper rufous underparts. **Voice.** Thin, high-pitched monosyllable.

**Habitat.** Rivers and streams with densely forested or scrub-lined banks, also *Nipa* palm swamps and mangroves near coast; from sea-level to 1000 m.

**Food and Feeding.** Small fish, and aquatic insects and larvae. Perches on rocks and overhanging vegetation; dives steeply into water for prey, then returns to perch and beats prey before swallowing it.

**Breeding.** Lays in Mar-May on Luzon and Mindoro. Nest a burrow in a riverbank. No other information.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Generally uncommon, but common in some localities; regularly recorded at Angat Water Catchment Area, near Manila, and also present in Quezon National Park, Luzon. More information is needed about its status and biology.

**Bibliography.** Brooks, Magsalay *et al.* (1995), Danielsen *et al.* (1994), Delacour & Mayr (1946), Dickinson *et al.* (1991), Evans, Dutton & Brooks (1993), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Gilliard (1950a), Gonzales (1983), Goodman & Gonzales (1990), Inskipp *et al.* (1996), Kennedy *et al.* (2000), Knowles & Nitehen (1995), McGregor (1905), duPont (1971), Tomlinson (2000), Whitehead (1899).

## 74. Small Blue Kingfisher

### *Alcedo coerulescens*

**French:** Martin-pêcheur aigue-marine **Spanish:** Martin Pescador Azulado  
**German:** Türkisfischer

**Other common names:** Caerulean Kingfisher

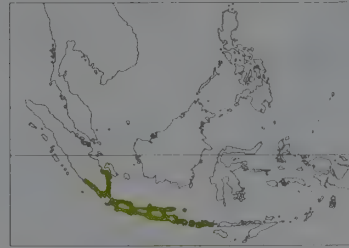
**Taxonomy.** *Alcedo caerulescens* Vieillot, 1818, Timor; error = Java.

May be closely related to *A. pusilla*. Monotypic.

**Distribution.** S Sumatra through Java, Kangean Is and Bali to Lombok and Sumbawa; recently recorded on Flores.

**Descriptive notes.** 13 cm. Male head and upperparts greyish azure-blue, white supraloral patch and neck patch, brilliant silvery-azure rump; white underparts, breast with well-marked azure-blue band; bill black, red-brown base of lower mandible; iris dark brown; legs and feet red-brown. Female duller, greener than male, breastband narrower and less distinct. Juvenile duller, blues greyer, breastband not distinct. **Voice.** High-pitched, repeated "ti ti ti", or 2-note "tew-tew" given in flight.

**Habitat.** Streams, canals, ponds, swamps, tidal estuaries, mudflats, mangroves, fish ponds, flooded paddyfields; from coast up to 800 m.



**Food and Feeding.** Aquatic insects, crustaceans and small fish. Sits on a low perch over-looking water or mudflats, and dives into water for prey. Also takes prey from more open waters, lacking perches, by hovering 2-4 m above the surface for c. 30 seconds before either diving into the water or returning to its perch.

**Breeding.** Lays in Apr-Jun, Aug and Oct in Java. Only nest reported was an inclined tunnel, dug by both of pair, in a steep bank by a paddyfield. Clutch 3-6 eggs. No other information.

**Movements.** Presumably sedentary, but single record in 1997 from Flores, where not found

previously, may suggest some vagrancy.

**Status and Conservation.** Not globally threatened. Widely distributed and common in many localities, as in Suwung Fishponds and Bali Barat National Park, Bali, and Baluran National Park and Pulau Dua Reserve, Java. Probably recently colonized S Sumatra from Java.

**Bibliography.** Andrew (1992), van Balen (1998), Coates & Bishop (1997), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Hellebrekers & Hoogerwerf (1967), Holmes (1977, 1996), Holmes & Nash (1989), Hoogerwerf (1949e, 1953, 1970), Hoogerwerf & Siccama (1938), Inskipp *et al.* (1996), Johnstone *et al.* (1996), Knowles & Nitehen (1995), Long *et al.* (1992), MacKinnon (1988), MacKinnon & Philipps (1993), van Marle & Voous (1988), Mason (1989), Nash & Nash (1985), Parrott & Andrew (1996), Rensch (1931), Sargeant (1997), Verheugt *et al.* (1993), Verhoeve & Holmes (1999), White & Bruce (1986).

## 75. Blue-banded Kingfisher

### *Alcedo euryzona*

**French:** Martin-pêcheur à large bande **Spanish:** Martin Pescador Bandeado  
**German:** Brustbandeisvogel

**Other common names:** Broad-zoned Kingfisher

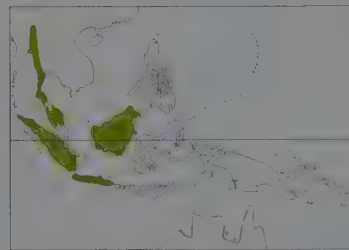
**Taxonomy.** *Alcedo euryzona* [sic] Temminck, 1830, Java.

Two subspecies recognized.

**Subspecies and Distribution.**

*A. e. peninsulæ* Laubmann, 1941 - S Myanmar and W Thailand S to Sumatra, and Borneo.

*A. e. euryzona* Temminck, 1830 - Java.



**Descriptive notes.** 17 cm; male 40-45 g, female 38-49 g. Male of nominate race has black crown, cheeks and hindneck with blue tips, white or buffy loreal spot and neck patch; lower mantle and back brilliant blue, rump silvery azure; scapulars, wings and tail blue-washed black with small blue spots on wing-coverts; underparts white, blue breastband; bill grey-black; iris dark brown; legs and feet orange-brown. Female has browner upperparts, rufous loreal spot and neck patch, rufous belly, orange-red lower mandible. Juvenile duller, male pale rufous underparts. Race *peninsulæ* male has variably mottled breastband, female has

orange-brown breast without band and is paler rufous on abdomen. **Voice.** High-pitched "cheep" given in flight.

**Habitat.** Slow-flowing streams and larger rivers in primary rainforest, locally also mangroves, and sometimes found in forest up to 100 m away from stream; from sea-level to 850 m, mainly in lowlands, but locally to 1500 m.

**Food and Feeding.** Fish, also crustaceans, insects and larvae, and small lizards. Hunts from a low perch near stream in forest, frequently moving to another perch.

**Breeding.** Lays in Jan-Mar and Jun, in Mar-Apr in Java. Nest-burrow dug into bank of small stream in dense forest. Clutch 3-5 eggs. No other information available.

**Movements.** Presumably sedentary. Two birds ringed at Selangor, in Peninsular Malaysia, were recaptured within 3 months and 10 months, respectively.

**Status and Conservation.** VULNERABLE. Locally fairly common in Peninsular Malaysia and in Borneo, rare in Myanmar, and uncommon in Thailand and Sumatra; no recent records from Java. Recorded in several protected areas: in Way Kambas National Park in Sumatra, in Gunung Palung National Park and Kutai National Park in Kalimantan, in Danum Valley Conservation Area in Sabah, in Similajau National Park in Sarawak, and in Taman Negara National Park in Peninsular Malaysia. Has undergone rapid decline as lowland forest has been cleared, and likely to continue to suffer from ongoing habitat destruction throughout its range. Logging and other disturbance may pollute essential streams and rivers in its habitat. May be able to survive at higher elevations, where habitat loss and degradation less severe.

**Bibliography.** Andrew (1992), van Balen (1999), Bartels (1938), Brown (1979), Duckworth *et al.* (1997), Ford & Davison (1995), Hellebrekers & Hoogerwerf (1967), Holmes (1996, 1997), Hoogerwerf (1948b), Inskipp *et al.* (1996), Jayarajasingam & Pearson (1999), Lekagul & Round (1991), Long *et al.* (1992), MacKinnon (1988), MacKinnon & Philipps (1993), van Marle & Voous (1988), McClure (1998), Medway & Wells (1976), Mees (1971), Parrott & Andrew (1996), Pearson (1975c), Riley (1938), Robson (2000a), Smythies (1986, 1999), Stattersfield & Capper (2000), Verheugt *et al.* (1993), Vowles & Vowles (1984), Wells (1985, 1999), Wilkinson, Dutton & Sheldon (1991).



ssp  
*quadribachys*

ssp *azurea*

ssp *guentheri*

ssp *ruficollaris*

ssp *affinis*

ssp *ochrogaster*

ssp *pusilla*

ssp *richardsi*

ssp *bougainvillei*

ssp *meninting*

ssp *atthis*

ssp *rufigaster*

ssp *floresiana*

ssp *hispidoides*

inches 3  
cm 8



## 76. Shining-blue Kingfisher

### *Alcedo quadibrachys*

**French:** Martin-pêcheur azuré **German:** Schillereisvogel **Spanish:** Martin Pescador Brillante  
**Other common names:** Shining Kingfisher

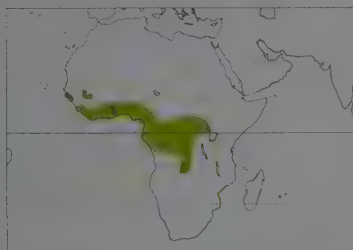
**Taxonomy.** *Alcedo quadibrachys* Bonaparte, 1850, Guinea.

Forms ■ superspecies with *A. azurea* and *A. websteri*, and possibly also *A. meninting*. Two subspecies recognized.

#### Subspecies and Distribution.

*A. q. quadibrachys* Bonaparte, 1850 - Senegambia to W Nigeria (E to R Niger).

*A. q. guentheri* Sharpe, 1892 - SE Nigeria E to extreme S Sudan and Uganda (L Victoria), and S to N Angola and NW Zambia.



**Descriptive notes.** 16 cm; male 33-36 g, female 32-40 g. Male nominate race buffy loreal spot, cream neck patch, head and wings black with glossy ultramarine tips, mantle to uppertail-coverts brilliant purple-blue, tail blue-black; creamy chin and throat, small purple-blue collar at side of breast, remaining underparts orange-chestnut; bill black; iris dark brown; legs and feet orange-red. Female dark red base of lower mandible. Juvenile paler crown, paler orange underparts, dusky mottling forming breastband, white tip of bill. Race *guentheri* paler back colour, brilliant cobalt-blue, pale azure-blue rump. **VOICE.** High-

pitched "cheet" given mainly in flight, and repeated high-pitched "seet-seet-seet-seet"; nestlings make fizzling noise when alarmed.

**Habitat.** Lagoons, estuaries and mangroves on the coast, and reedbeds, papyrus swamps, streams, rivers, ponds, lakes and reservoirs in forest, savanna and farmland; mainly in lowlands, to 1800 m in Zaire.

**Food and Feeding.** Mainly fish to 6 cm in length, also aquatic insect larvae and small crabs. Searches for prey from a perch in trees or overhanging branches, 1-2 m above the water; dives steeply into water and return to perch with its catch.

**Breeding.** Lays in Sept in Nigeria, in Nov in Cameroon, in Dec-Mar in Gabon, in Mar in Congo, in Dec, Feb and Apr-Jul (mainly May) in Uganda, and in Oct in NE Zaire. Pair digs a burrow 40 cm long in a vertical streamside bank, or in side of a gravel pit or saw-pit; nest can be up to 1 km from a stream. Clutch 4-6 eggs. No other information.

**Movements.** Generally sedentary; some indication of seasonal variation in numbers, e.g. absence during Mar-May in Lagos (S Nigeria), and also irregular movements which probably involve dispersal by juveniles.

**Status and Conservation.** Not globally threatened. Widespread and common in forested areas. In Ghana, 50 pairs were counted along 48 km of river. No obvious threats.

**Bibliography.** Allport *et al.* (1989), Aspinwall & Beel (1998), Bannerman (1933, 1953), Barlow *et al.* (1997), Bates (1930), Bengtsson (1975), Bennun & Njoroge (1996, 1999), Benson (1964), Benson *et al.* (1971), Bouet (1961), Brunel (1958), Cave & Macdonald (1955), Chapin (1939), Cheke & Walsh (1996), Christy & Clarke (1994), Clancey (1992), Colston & Curry-Lindahl (1986), Curry-Lindahl (1960), Dean (2000), Dekeyser & Derivot (1966), Demey *et al.* (2000), Dowsett (1990), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Dowsett-Lemaire & Dowsett (1999, 2000), Elgood *et al.* (1994), Field (1999), Friedmann (1978), Friedmann & Williams (1971), Fry (1980a), Fry *et al.* (1988), Gartshore (1989), Gartshore *et al.* (1995), Gatter (1988, 1997), Gee & Heigham (1977), Germain *et al.* (1973), Greig-Smith (1976), Grimmes (1987), Hamel (1980), Heigham (1976), Hockey (1997), Jackson & Solater (1938), Leonard (1998a), Lewis & Pomeroy (1989), Mackworth-Præd & Grant (1957, 1962, 1970), McCausland (1965), Meadows (1976b), Meadows *et al.* (1975), Morel & Morel (1990), Pinto (1983), Rand (1951), Robertson (1992), Rodwell *et al.* (1996), Salomonsen (1934), Serle (1965), Serle *et al.* (1977), Short *et al.* (1990), Snow (1978, 1979), Turner, Zimmerman & Pearson (1991), Zimmerman *et al.* (1996).

## 77. Azure Kingfisher

### *Alcedo azurea*

**French:** Martin-pêcheur à dos bleu **German:** Azurfischer **Spanish:** Martin Pescador Azul  
**Other common names:** Blue/Creek/Purple/River(!)/Water Kingfisher

**Taxonomy.** *Alcedo azurea* Latham, 1801, Norfolk Island; error = New South Wales.

Sometimes placed in genus *Alcyon*, or in *Ceyx*. Forms a superspecies with *A. quadibrachys* and *A. websteri*, and possibly also *A. meninting*. In past, race *ruficollaris* inexplicably and erroneously listed under *Todiramphus sanctus*. Race *yamdenae* sometimes included in *ruficollaris*; birds from Aru Is formerly separated from *lessonii* as race *wallaceana*. Seven subspecies currently recognized.

#### Subspecies and Distribution.

*A. a. affinis* (G. R. Gray, 1860) - Morotai, Halmahera and Bacan (N Moluccas).

*A. a. lessonii* (Cassin, 1850) - W Papuan Is and lowland S New Guinea E to D'Entrecasteaux Is, also Aru Is.

*A. a. ochrogaster* (Reichenow, 1903) - islands in Geelvink Bay, and N New Guinea from R Mamberano E to Astrolabe Bay, S to Wahgi Valley, also Karkar I and Admiralty Is.

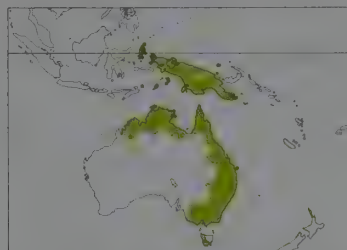
*A. a. yamdenae* (Rothschild, 1901) - Romang (E Lesser Sundas) and Tanimbar Is.

*A. a. ruficollaris* (Bankier, 1841) - N Australia, from Kimberley E to Cooktown.

*A. a. azurea* Latham, 1801 - E & SE Australia, from Cooktown S to Victoria.

*A. a. diemenensis* (Gould, 1846) - Tasmania.

**Descriptive notes.** 18 cm; male 29-32 g, female 31-35 g. Male nominate race rufous loreal spot, large white neck patch, deep ultramarine-blue upperparts extending as patch on side of breast; chin and throat buffish-white, breast and belly orange-rufous, prominent violet wash on flanks; bill black, extreme tip whitish; iris dark brown, legs and feet orange-red. Female slightly duller than male, less violet on flanks. Juvenile duller, paler, bill with large whitish tip. Races show minor differences in size and colour compared with nominate: *affinis* has brighter blue, bill tip reddish, longer wing; *yamdenae* like previous, but smaller; *lessonii* slightly darker upperparts, paler underparts, less vio-



let flanks: *ochrogaster* even paler below; *ruficollaris* has richer colours, shorter wing and tail, longer bill; *diemenensis* larger, crown and rump darker, more violet-blue. **VOICE.** Short, repeated, high-pitched "pseet" in flight; also continuous high-pitched whistle by several birds during wing-waving display; repeated shrill calls when alarmed; young have twittering begging call or thin feeble squeaks.

**Habitat.** Coastal wooded watercourses, estuaries, tidal creeks and lagoons, mangroves, *Melaleuca* and sago swamps, also inland at wooded creeks, rivers, lakes, swamps, and forest streams and pools; rarely, on mudflats or

sandy beaches, irrigation canals, riverside parks and duck ponds. Sea-level and lower altitudes, to 1520 m in New Guinea.

**Food and Feeding.** Mainly small fish (Cyprinidae, Salmonidae); also crustaceans (Malacostraca, Parastacidae), and water beetles (Coleoptera), bugs (Hemiptera), dragonflies (Anisoptera), occasionally locusts (Orthoptera), spiders, small frogs and tadpoles. Sits on a perch 1-10 m above water, occasionally bobbing head or cocking tail, or moving whole body up and down; then plunges into water for prey and returns with it to perch, where the prey is battered before being swallowed head first; sometimes hovers briefly before diving into the water. In a deep dive the whole body is streamlined, but in a shallow one the wings are half-open. Occasionally takes insects in flight, or terrestrial beetles from the ground. Will follow a foraging platypus (*Ornithorhynchus anatinus*) to catch fish and shrimps disturbed by it.

**Breeding.** Lays in Sept-Apr in N Australia, in Aug-Feb in S Australia; double-brooded in SE Australia (Victoria). Territorial, pair occupying 200-1600 m of suitable river or shoreline. Nest excavated by both of pair, in bank of stream, river, lake or billabong, sometimes in mangroves, or occasionally in soil around roots of an uprooted tree or in road verge, which can be several 100 m from water; in Australia, uses bank 0.9-3 m high, with tunnel 0.6-3 m above water; tunnel 15-88 cm long, 4-7 cm in diameter, and slightly inclined, ending in unlined chamber 12-15 cm in diameter. Clutch 4-7 eggs, usually 5 or 6 in Australia; both parents incubate, period 20-22 days; both feed chicks 21-35 days; nest becomes fouled with faeces and food remains, and adults often bathe after brood-feeding; adults continue to feed young for a short time after fledging, and while incubating second clutch of eggs. Nests sometimes destroyed by floods; nest contents occasionally preyed on by brown snake (*Demansia*). A ringed bird in Australia lived for over 11 years.

**Movements.** Mainly sedentary, but juveniles disperse varying distances, and some adults wander widely when not breeding, resulting in sporadic occurrences. Seasonal movements in some localities, e.g. more common in austral summer in Tasmania and parts of Victoria. In Australia, 99% of 175 recoveries of ringed birds were less than 10 km from ringing site, and longest movement only 10 km.

**Status and Conservation.** Not globally threatened. Widely distributed, in a range of habitats; widespread in N, becoming more coastal in S Australia. Some mortality caused by birds colliding with windows; greater threat from river pollution, and from increased turbidity caused by human activity and introduced European carp (*Cyprinus carpio*). Was formerly shot for its plumage.

**Bibliography.** Andrew (1992), Barker & Vestjens (1989), Beehler (1978), Beehler *et al.* (1986), Bell (1982a), Beruldsen (1990), Blakers *et al.* (1984), Boekel (1980), Burnett (1996), Clancy (1980), Coates (1985), Coates & Bishop (1997), Deignan (1964), Diamond (1972), Diamond & LeCroy (1979), Eastman (1970), Forshaw & Muller (1978), Frith & Hitchcock (1974), Garnett (1993), Gyldestolpe (1955b), Hall (1974), Haselgrove (1975), Heinrich (1956), Higgins (1999), Hoogerwerf (1971), Ingram (1976), Johnstone & Storr (1998), Johnstone *et al.* (1977), Keast (1977), Lindsey (1992), Macdonald (1988), Mackay (1970, 1977, 1980), Marshall (1931), Mayr & Meyer de Schauensee (1939), McAllan & Bruce (1989), McCulloch (1973), Mees (1982), Peekover & Filwood (1976), Pizzey & Knight (1997), Rand (1942a), Rand & Gilliard (1967), Redmayne (1996), Ripley (1964), Rose (1980), Schodde & Hitchcock (1968), Schodde & Mason (1976), Schodde & Tidemann (1986), Simpson & Day (1998), Storr (1973, 1977, 1980), Strahan (1994), Thomas (1979), Troughton & Wray (1994), Trounson & Trounson (1987), Watts (1999), White & Bruce (1986), Woinarski (1993).

## 78. Bismarck Kingfisher

### *Alcedo websteri*

**French:** Martin-pêcheur des Bismark **Spanish:** Martin Pescador de las Bismarck  
**German:** Bismarckfischer

**Other common names:** Bismarck Pygmy-kingfisher, Island Webster's Kingfisher

**Taxonomy.** *Alcyon websteri* Hartert, 1898, New Hanover.

Sometimes placed in the genus *Ceyx*. Forms a superspecies with *A. quadibrachys* and *A. azurea*, and perhaps also *A. meninting*. Monotypic.

**Distribution.** Bismarck Archipelago, on New Hanover, New Ireland, Lihir Is, Umboi and New Britain; sight record from Feni.



**Descriptive notes.** 22 cm; male 54-57 g, female 67 g. Both sexes have white loreal feathers; large creamy-white neck patch, greenish-blue head and upperparts, extending as patch on side of breast; underparts creamy white, pale orange wash on breast; bill black with whitish tip; iris black; legs and feet grey-brown. Female appears to lack patches on sides of breast, and may have richer buff underparts. Juvenile not described. **VOICE.** Loud whistle, louder, stronger and less sibilant than that of *A. atthis*.

**Habitat.** Lowland forest streams and rivers, less commonly streams in degraded or logged forest, generally preferring slow-flowing water-

courses; possibly also at lakes fringed by forest (e.g. 1 record from L Hargy, New Britain), but not at more open lakes fringed by reedbeds or marshes. Occurs from sea-level to c. 250 m or perhaps slightly higher. Apparently replaced by *A. atthis* along larger rivers and at most lakes, as well as in mangroves; replaced by *Ceyx lepidus* along smaller streams.



**Food and Feeding.** Fish, crayfish and shrimps, also insects and larvae. Often perches on dead tree limbs, close to water, then dives into water to catch prey and returns with it to perch.

**Breeding.** A laying female was collected in Nov on Lihir Is. No other information on breeding available.

**Movements.** Presumably sedentary.

**Status and Conservation.** VULNERABLE. Restricted-range species: present in New Britain and New Ireland EBA. Little-known kingfisher. Few records of this species exist, although little information available from the area, and species might have been overlooked; it was found still to be present in 1997 on all 5 islands in its range. Population estimated to be small, and probably declining as a result of extensive habitat destruction and deterioration. Its evident dependence on extreme lowland forest means that further loss of habitat could represent a severe threat; on largest island, New Britain, in particular, large areas have already been, or are scheduled to be, logged or cleared to replace natural forest with commercial oil palm (*Elaeis guineensis*) plantations. In New Hanover, reported as locally common in Woi R and some tributaries; also seen in Habiuk R in an area previously disturbed by logging. Deterioration of water quality in rivers from soil run-off in partially cleared forest is likely to be a significant problem. Further research is needed to determine this species' tolerance of degraded habitats, and to provide accurate assessment of its current population. Information also required on its breeding biology.

**Bibliography.** Clay (1994), Coates (1985), Dutson (2000), Eastwood & Hicks (1998), Forshaw & Cooper (1983, 1985), Fry *et al.* (1992), Gilliard & LeCroy (1967a), Gregory (2000), Knowles & Nitchen (1995), Leavesley & Leavesley (1999), Stattersfield & Capper (2000), Stattersfield *et al.* (1998).

## 79. Little Kingfisher

### *Alcedo pusilla*

**French:** Martin-pêcheur poucet **German:** Mangrovfischer **Spanish:** Martín Pescador Menudo  
**Other common names:** Mangrove Kingfisher(!); Ramsay Kingfisher (*ramsai*)

**Taxonomy.** *Ceyx pusilla* Temminck, 1836. Lobo, Triton Bay, New Guinea. Sometimes placed in genus *Ceyx* or in *Alcyon*. Possibly closely related to *A. coerulescens*. Nine subspecies recognized.

**Subspecies and Distribution.**

*A. p. halmaherae* (Salomonsen, 1934) - Halmahera, Bacan and Obi (N Moluccas).

*A. p. pusilla* (Temminck, 1836) - W Papuan Is, Kai Is and Aru Is through S New Guinea to D'Entrecasteaux Is (Goodenough, Fergusson), and S to islands in Torres Strait, and NE Cape York Peninsula.

*A. p. laetior* (Rand, 1941) - N New Guinea, from Geelvink Bay E to Astrolabe Bay.

*A. p. masauji* (Mathews, 1927) - Bismarck Archipelago, on New Hanover, New Ireland, Tabar Is, Umboi and New Britain.

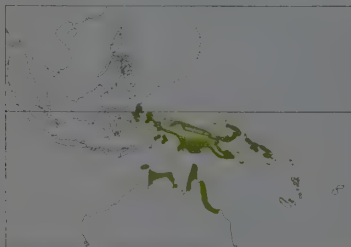
*A. p. bougainvillei* (Ogilvie-Grant, 1914) - Solomon Is, from Buka and Bougainville E to Choiseul, Santa Isabel and Florida Is.

*A. p. richardsi* (Tristram, 1882) - New Georgia Group (WC Solomons).

*A. p. aolae* (Ogilvie-Grant, 1914) - Guadalcanal (E Solomons).

*A. p. ramsayi* (North, 1912) - N Australia, from Melville I and R Victoria E to W Cape York Peninsula.

*A. p. halli* (Mathews, 1912) - NE Queensland, from R Endeavour S to Keppel Bay.



band; *halli* slightly larger, upperparts more purplish-blue; *halmaherae* paler; *masauji* darker, complete pectoral band; *bougainvillei* larger, paler, sometimes with scaly pectoral band; *richardsi* blue wings stronger pectoral band, blue undertail-coverts; *aolae* incomplete pectoral band, white undertail-coverts with blue tips. **VOICE.** High-pitched, repeated "tsee" or "peep" given in flight; at the nest other ticking notes also given; nestlings have churring or buzzing calls; shrill calls against intruders by parents with young.

**Habitat.** Coastal mangroves, *Melaleuca* and *Nipa* swamps, forested tidal or freshwater creeks, alluvial forest, pools, streams, rivers or gutters in woodland, forest and secondary growth; occasionally in gardens surrounded by rainforest, and coral cay with tall mangroves. Sea-level to 750 m in Queensland. Restricted to coast in Melanesia, where perhaps excluded from rivers and forest by *A. atthis* and *Ceyx lepidus*.

**Food and Feeding.** Tiny fish, crustaceans, shrimps (Malacostraca), and aquatic beetles (Coleoptera) and insect larvae. Perches quietly on a low perch less than 2 m over water, occasionally bobbing head; makes shallow dive, completely submerging, and then returns to perch to swallow prey.

**Breeding.** Lays in Feb in Northern Territory, in Oct-Apr in Queensland, in Jan-Apr in Papua New Guinea, and in Jun on Bougainville. Nest-tunnels excavated in streamside bank or riverbank, in soil among roots of fallen tree, in rotting mangrove or paperbark stump, or in terrestrial or arboreal termitarium. 8-15 m above ground; one tunnel was 15 cm long, 3 cm wide, ending in chamber 13 cm wide and 10 cm high. Clutch 3-5 eggs in Australia; incubation and fledging periods not recorded; both parents feed the brood, in one case every 5 minutes with fish from a swamp 300 m away, in another 2 fish (c. 5-cm long) per young per hour; 9 days after leaving nest young dive clumsily for fish, although still being fed by parents; parents with young swoop at intruders while emitting shrill calls.

**Movements.** Presumably sedentary, with local movements into flooded areas during the wet season. Recoveries of 6 ringed individuals were all less than 10 km from ringing site.

**Status and Conservation.** Not globally threatened. Widespread and locally common. In Australia, density of 0.08 birds/ha in mangroves in Northern Territory. Some subspecies, however, have restricted ranges, and these may possibly be threatened by extensive clearance of mangroves and by habitat alteration along coasts; no records of the Guadalcanal race *aolae* have been published since several decades ago.

**Bibliography.** Andrew (1992), Barker & Vestjens (1989), Barnard (1926), Beecher *et al.* (1986), Bell (1970c, 1982a), Beruldsen (1990), Blaber (1990), Blakers *et al.* (1984), Bravery (1970), Broadbent (1910), Coates (1985), Coates &

Bishop (1997), Doughty *et al.* (1999), Dutson (2000), Eastman (1970), Forshaw & Muller (1978), Frith & Hitchcock (1974), Galbraith & Galbraith (1962), Gilliard & LeCroy (1966), Griffin (1995), Hadden (1981), Hall (1974), Haselgrove (1975), Heinrich (1956), Higgins (1999), Inskipp *et al.* (1996), Isherwood, Edwards *et al.* (1998), Isherwood, Willis *et al.* (1997), Johnson & Hooper (1973), Lamothe (1990), Lindsey (1992), Macdonald (1988), MacGillivray (1910, 1911, 1914, 1918), Mackay (1970), Mayr (1945), Mayr & Rand (1937), McLean (1996), Mees (1965), Miller (1932), Noske (1996), Peckover & Filewood (1976), Pizzey & Knight (1997), Rand (1942a, 1942b), Rand & Gilliard (1967), Schodde (1977), Schodde & Tidemann (1986), Simpson & Day (1998), Storr (1977, 1984b), Strahan (1994), Thompson (1984), Trounson & Trounson (1987), Webb (1992), White & Bruce (1986).

## 80. Blue-eared Kingfisher

### *Alcedo meninting*

**French:** Martin-pêcheur méninting **Spanish:** Martin Pescador Meninting  
**German:** Menintingeisvogel  
**Other common names:** Deep-blue/Malaysian Kingfisher

**Taxonomy.** *Alcedo Meninting* Horsfield, 1821. Java.

May be part of the superspecies that includes *A. quadibrachys*, *A. azurea* and *A. websteri*. Some uncertainty over races in S India: possibly only *colartii* present there, with *phillipsi* confined to Sri Lanka. Race *scintillans* intergrades with *verreauxii*. Various other described races include *laubmanni* (E India), *amadoni* (Palawan), *subviridis* (Banyak Is, Nias I), *callima* (Batu Is) and *proxima* (Mentawai Is), but these are not now considered sufficiently distinct. Six subspecies currently recognized.

**Subspecies and Distribution.**

*A. m. colartii* Stuart Baker, 1919 - S India (except Kerala), and Nepal E to Myanmar, Thailand and Indochina.

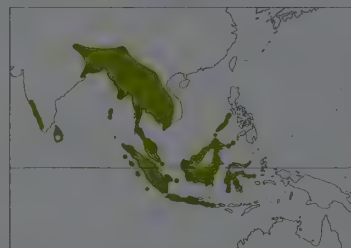
*A. m. phillipsi* Stuart Baker, 1927 - Kerala and Sri Lanka.

*A. m. rufigastria* Walden, 1873 - Andaman Is.

*A. m. scintillans* Stuart Baker, 1919 - S Myanmar (S Tenasserim) and N peninsular Thailand.

*A. m. verreauxii* De La Berge, 1851 - S peninsular Thailand and Malaysia S to Riau Archipelago, Bangka and Belitung, and E to Borneo, Palawan, Sulu Is.

*A. m. meninting* Horsfield, 1821 - Sumatra, including islands off W coast, and Java E to Lombok, also Sulawesi and Banggai and Sula Is.



**Descriptive notes.** 17 cm; 16-23 g. Male nominate race rufous frontal spot, white blaze on side of neck; head and neck ultramarine-blue, closely banded with darker blue; upperparts, wings and tail glossy dark blue, paler band down centre of back and rump; whitish chin and throat, rufous underparts; bill black with brownish-red base; iris dark brown; legs and feet orange-red. Female more red on lower mandible, in some individuals entire bill red. Juvenile duller, rufous cheeks and ear-coverts, dusky tips to breast feathers, black bill with white tip. Races vary slightly in size and colour: *verreauxii* darker; *scintillans* and *rufigastria* increasingly paler than nominate; *colartii* blues greener; *phillipsi* larger, darker. **VOICE.** Single, high-pitched note, "tjet" or "trree-tee", like that of *A. atthis* but sharper and less shrill; rapid chatter when perched.

**Habitat.** Streams, creeks, channels and estuaries in evergreen and wet deciduous forest, bamboo-forest and dense mangroves; also regenerating and tall secondary forest, forest edge, and occasionally found at streams through tree plantations. Uses habitats similar to, but denser than, those of *A. atthis*. Sea-level to 1000 m.

**Food and Feeding.** Fish, crustaceans, and insects and larvae, including dragonflies (Odonata). Perches near water, searching for prey with head bobbing and tail flicking; dives vertically into water and returns to perch with the catch, which is struck on perch before being swallowed head first. Sometimes flies from perch to perch, apparently catching aerial insects.

**Breeding.** Lays in Apr-Aug, mainly May-Jun, in N India, in Jan in Kerala, in Apr-Jul in Myanmar, in Feb but mainly in May-Jun in Peninsular Malaysia, in Jan-Jul in Andaman Is, in Apr in Sumatra, in Dec-Aug in Borneo, and in Jan, Mar-Jun, Oct and Dec in Java; some pairs double-brooded in India. Nest dug in sloping or vertical earth bank, soil dump or road cutting, always in forest and near stream, tunnel 30-100 cm long and 5 cm wide, ending in nest-chamber 12-14 cm wide and 10-12 cm high. Clutch 3-7 eggs; both sexes incubate and both feed the young; no information on incubation and fledging periods.

**Movements.** Sedentary; birds ringed at Selangor, in Peninsular Malaysia, were recaptured frequently up to 16 months later.

**Status and Conservation.** Not globally threatened. Widespread, but seldom common. Occurs in many protected areas throughout range, as Chitwan National Park (Nepal), Kaziranga National Park (Assam), Uda Walawe National Park (Sri Lanka), Khao Yai National Park (Thailand), Barito Ulu National Park (Kalimantan), St Paul Subterranean National Park (Palawan) and Way Kambas National Park (Sumatra). Its preference for densely covered streams makes it vulnerable to deforestation.

**Bibliography.** Abdulali (1972b), Ali (1977, 1996), Ali & Ripley (1983), Baker (1918, 1934a, 1934b), van Balen (1996, 1999), Burton (1978b), Chasen & Hoogerwerf (1941), Coates & Bishop (1997), Daniels (1997), Deignan (1945), Dickinson *et al.* (1991), Duckworth & Kelsch (1988), Duckworth, Salter & Khounboline (1999), Duckworth, Tizard *et al.* (1998), Gore (1968), Gregory-Smith (1995, 1997), Grimmer *et al.* (1998), Harrison (1999), Harvey (1990), Hellebrekers & Hoogerwerf (1967), Henry (1998), Hoffmann (1998), Holmes, P & Wood (1980), Hoogerwerf (1949a, 1949c, 1970), Hoogerwerf & Siccama (1938), Inskipp & Inskipp (1991), Jayewardene (1989), Jayarajasingam & Pearson (1999), Johnstone *et al.* (1996), Junge (1936), Kennedy *et al.* (2000), Lamsfuss (1998), Lekagul & Round (1991), Lim Kim Seng (1992), Long *et al.* (1992), MacKinnon & Phillips (1993, 2000), van Marle & Voous (1988), McClure (1998), Medway & Wells (1976), Mees (1986), Meyer de Schauensee (1984), Meyer de Schauensee & Ripley (1940), Mukherjee & Dasgupta (1986), duPont (1971), duPont & Rabot (1973a), Riley (1938), Ripley *et al.* (1988), Robson (2000a), Smythies (1986, 1999), Stepanyan (1986), Stresemann (1940), Tikader (1984), Vowles & Vowles (1984), Wells (1999), White & Bruce (1986), Zhao Zhengjie (1995).

## 81. Common Kingfisher

### *Alcedo atthis*

**French:** Martin-pêcheur d'Europe **German:** Eisvogel **Spanish:** Martín Pescador Común  
**Other common names:** River(!)/European/Eurasian Kingfisher, Kingfisher

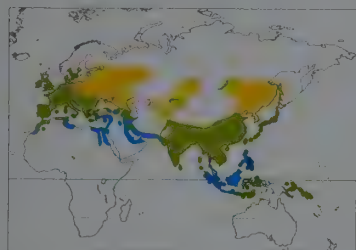
**Taxonomy.** *Gacula Atthis* Linnaeus, 1758. Egypt.



Forms a superspecies with *A. semitorquata*, with which formerly considered conspecific; also closely related to *A. hercules*, range of which overlaps in NE India and SE Asia. Populations in C Asia, Afghanistan and Kashmir sometimes separated as *pallasi* on basis of shorter bill and paler underparts, but they seem to fall within normal range of variation of nominate; proposed race *japonica* included within *bengalensis*. Seven subspecies currently recognized.

#### Subspecies and Distribution.

*A. a. isipda* Linnaeus, 1758 - S Norway, British Is and Spain (except S & E) E to W Russia and Romania; winters S to S Portugal, N Africa, Cyprus and Iraq.  
*A. a. athis* (Linnaeus, 1758) - NW Africa and S & E Spain E to Bulgaria, Afghanistan, NW India, C Siberia and NW China; winters S to Egypt, NE Sudan, Oman and Pakistan.  
*A. a. bengalensis* J. F. Gmelin, 1788 - C India E to SE Asia, S & E China (including Hainan), SE Siberia, E Mongolia and Japan; winters S to Greater Sundas, N Sulawesi, Sula Is, N Moluccas and Philippines.  
*A. a. taprobana* Kleinschmidt, 1894 - India S of R Godavari, and Sri Lanka.  
*A. a. floresiana* Sharpe, 1892 - Bali and Lesser Sundas E to Wetar and Timor.  
*A. a. hispidoides* Lesson, 1837 - Sulawesi, Moluccas and W Papuan Is, and coastal E New Guinea from R Sepik and R Aroa to D'Entrecasteaux Is and Louisiade and Bismarck Archipelagos.  
*A. a. salomonensis* Rothschild & Hartert, 1905 - Solomon Is (Buka and Bougainville E to San Cristobal).



**Descriptive notes.** 16 cm; male 23-35 g (*athis*), 29-45 g (*isipda*), 19-40 g (*bengalensis*), female 30-35 g (*athis*), 34-46 g (*isipda*), 20-30 g (*bengalensis*). In most of its range the only small blue kingfisher. Male nominate race rufous dorsal spot, black eyestripe, rufous ear-coverts, white neckstripe; crown and malar stripe barred blue and black; upperparts and tail brilliant azure-blue, wings dark greenish-blue with paler blue spots; white chin and throat, rufous underparts; bill black, gape red; iris dark brown; legs and feet orange-red. Distinguished from similar small *Alcedo* species by rufous ear-coverts. Female like male, but

lower mandible orange-red with black tip. Juvenile duller, greener than adult, paler below, dusky barring on breast, whitish tip of bill, black legs and feet. Race *isipda* slightly larger, blue crown, darker rufous underparts; *bengalensis* smaller, brighter; *taprobana* similar in size to previous, but upperparts bright blue, not green-blue; *floresiana* darker blues on upperparts, some blue feathers on rufous ear-coverts; *hispidoides* ear-coverts blue, purple tinges on hindneck and rump; *salomonensis* ear-coverts blue, more extensive purple-blue upperparts. Voice. Short, shrill "chee, chee" in flight; alarm a harsher "tji!" harsh grating "kritritrit" as threat; advertising call "tee titi titi titi"; song a mixture of whistles and warbles; begging call of female a plaintive "chee chee", excitement call "tsuk tsuk"; nestlings first make plaintive "cheep cheep", after 10 days becoming a churring, and at fledging a sharp "zipp" or "tschick" as contact.

**Habitat.** Still or gently flowing water with plentiful small fish, and with reeds, rushes or shrubs on the banks for perches, are essential aspects of the habitat. Streams, small rivers, canals and ditches preferred to open waterbodies, but also uses lakes, ponds and flooded gravel pits. Suitable banks for nesting required in breeding season, but nest-sites can be over 250 m from foraging waters. In winter becomes more coastal, frequenting also estuaries, harbours and rocky seashores. In tropical regions, is found in the lower reaches of rivers, often with densely vegetated banks, in creeks in mangroves, at swamps and wet grassland, and in large gardens. In E parts of range comes into contact with several other similar species, which may restrict its habitat selection.

**Food and Feeding.** Fish the main prey in Europe; include minnows (*Phoxinus*), sticklebacks (*Gasterosteus*), bullhead (*Cottus*), roach (*Rutilus*), barbel (*Barbus*), grayling (*Thymallus*), trout (*Salmo*), dace and chub (*Leuciscus*), perch (*Perca*), young pike (*Esox*), loach (*Cobitis*), *Noemacheilus*, carp (*Carassius*), gudgeon (*Gobio*), ruffe (*Acerina*), bleak (*Alburnus*), nase (*Chondrostoma*), and many other species up to 125 mm long. Also takes aquatic insects, including water-bugs (Hemiptera), water beetles (Dytiscidae), dragonfly nymphs and occasionally adults (Odonata), mayflies (Ephemeroptera), lacewings (Neuroptera), stoneflies (Plecoptera), caddis flies (Trichoptera); also flies (Diptera), butterflies and moths (Lepidoptera), amphibians (*Rana*), crayfish (*Astacus*), prawns (*Palaeomon*), shrimps (*Gammarus*) and isopods in winter. Very occasionally feeds on berries (*Rubus*, *Sambucus*) and stems of reed (*Phragmites*). In Britain and Ireland diet consisted of 60% fish, 20% insects and larvae, 5% crustacea, 5% tadpoles, and 5% molluscs; in Belgium, bullhead and loaches formed 96% of remains in pellets; elsewhere in Europe more variable diet, e.g. in Spain 78% fish, 10% crustaceans, 8% insects, 3% frogs. Wintering birds in Malaysia fed mainly on fish (60%) and shrimps (30%), with median prey length of 30 mm. Found to consume 50-60% of its body mass daily, requiring 38 successful dives; one bird ate 13-21 minnows daily, a total of 46 g. Perches for long periods, usually 1-2 m above the water, occasionally to 11 m, periodically turning around and bobbing head and body to gauge distance when food sighted; dives steeply and catches prey below water to maximum depth of 1 m; using its buoyancy and flapping the wings, it rises through water bill first and flies back to its perch, where the fish is held near the tail, beaten against perch several times, then positioned lengthways in bill and swallowed head first; larger prey given longer and more thorough beating, held by tail and head battered against perch. Prey sometimes become impaled on thorns or wire during beating and may be left. Sometimes takes prey from water surface, and where no perches available will hover before diving. Seen to follow a foraging smooth-coated otter (*Lutrogale perspicillata*) to feed on fish and other displaced aquatic animals. Insects taken in flight. In Nepal, dives from perch for fish were 38% successful, but 54% successful from hovering. In Malaysia, 90% of foraging was diving from perch, 2-6% from hovering, 0-9% from horizontal flight, and overall success rate was 53%. In Kashmir, most feeding activity during 10:00-12:00 hours and 17:00-19:00 hours, avoiding peak feeding times of *Ceryle rudis* and *Halcyon smyrnensis*, but in Malaysia no well-defined activity patterns. Several times each day regurgitates a small pellet of indigestible fish bones and insect parts.

**Breeding.** Lays in Mar-Jul (mainly Apr) in Britain, mainly May in Sweden; in Mar-May in Morocco and Iraq; in Apr-Jul in Kashmir; in Mar-Jun in N & C India, in Feb-Sept (mainly Mar-Apr) in S India, and in Nov-Jun in Sri Lanka; in Mar-Jun in Myanmar, in Jan-Feb and possibly Jun in Malaysia; in Mar-Aug in Japan; and in Jun in Papua New Guinea; normally 1 or 2 broods, occasionally 3 or 4 reared successively. Monogamous, but record of polygamy in Sweden. Solitary breeder; I record of a first-year male helper bringing food to a nest. Resident birds pair in autumn but retain separate territories of c. 1 km until spring, when they merge; territories defended by calling in flight and by displaying from perch, where sits quietly, crouches and stretches, swaying body from side to side, or sits very upright with neck outstretched, bill agape and wings drooping, before chasing off an intruder. Male courtship-feeds female before copulation. Nest usually in sandy, stone-free streamside bank, quarry, sandpit, peat cutting or earth bank, occasionally in hole in wall, rotten tree

stump, concrete tunnel in canal bank, terrestrial termitarium, or burrow of Sand Martin (*Riparia riparia*) or water vole (*Arvicola terrestris*); record from N India of grass nest used almost certainly erroneously; most nests 90-180 cm above water, within 50 cm of top of bank, occasionally up to 500 m away from water; both sexes excavate, taking 7-12 days, tunnel straight, inclined to up to 30°, usually 50-90 cm long, being longer in sandy or loam soil than in stony or clay soil (range 15-137 cm), 5-7 cm wide, ending in nest-chamber 9-17 cm wide and 11 cm high; several nests may be partly excavated until one completed. Clutch 3-10 eggs, usually 6-7; both sexes incubate during day, but only female at night, often 1-2 eggs fail to hatch from the parents inability to cover them. Incubating bird sits motionless, facing tunnel, generally produces a pellet, which is broken up with the bill; incubation period 19-21 days, starting with last or penultimate egg, hatching synchronous; both adults feed young, initially bringing small fish 1-2 cm long, later larger fish; chicks up to 10 days old given fish up to 3 cm long in nest-chamber, older chicks fed fish 5-8 cm long in nest-tunnel, each chick fed every 45-50 minutes when small, every 20-25 minutes at 12 days, and every 15-20 minutes at 18 days; nest becomes fouled with faeces and food remains, and adults regularly bathe after feeding; fledging period 23-27 days or more; c. 4 days after leaving nest juveniles make first dives, sometimes becoming waterlogged and drowning, but soon independent and are driven from breeding territory by adults; female sometimes lays second clutch in adjacent nest-hole before previous brood fledged, and final brood may revert to original nest-hole. Breeding success 80% in Britain, 54% in Switzerland, 58% in Germany; mean lifetime fledgling production 9.8 for males and 9.7 for females in Germany, birds using preferred breeding sites having higher levels of lifetime production; nests preyed on by mustelids, including badgers (*Meles meles*) digging into nest-chamber, also by foxes (*Vulpes vulpes*). Mean annual mortality of 71-73% for adults and 78-79% for fledglings; longevity of 4 years and 11 months recorded in Netherlands and 4 years and 6 months in Britain.

**Movements.** N populations, in areas where freezing conditions in winter, regularly migrate S, generally staying within species' breeding range; populations in C Europe migrate in severe winters, and S populations (e.g. in Spain) are mainly sedentary. Distance moved varies, up to 250 km in Britain, 500 km in France and Belgium, 1500 km in Czechoslovakia, to 3000 km in Russia; non-breeding birds present in N Africa Sept-Apr and in Sudan Oct-Mar. In Hokkaido (N Japan), birds depart in mid-Sept and return late Apr or early May. One ringed in Korea was recovered 2 months later in Luzon, in N Philippines. In S Malay Peninsula, birds were netted at Fraser's Hill only during Aug-Oct, but at Selangor they were present Aug-Mar. Migrates mainly at night, and pronounced movements evident along Mediterranean shores and over Malaysian mountains in autumn; during migration may form small flocks. Wintering birds establish territories, and juveniles may stay together as pairs or groups.

**Status and Conservation.** Not globally threatened. Widely distributed and common in many regions, but sensitive to river pollution and river management. Population in W Europe estimated to be 10,000-15,000 pairs, and in whole of Europe 100,000 pairs; twice that number estimated for Asia and Melanesia. Mean density 6.6 birds/km in favoured sites in England; up to 8/km on channels and lagoons in mangroves in Peninsular Malaysia, where an estimated 8,000-10,000 birds use 800 km of coastline. Has increased in Sweden and Denmark in 20th century, but elsewhere in Europe some recent declines owing to river pollution. Monitoring from 1963 to 1989 in Britain showed significant levels of organochlorine pesticides (HEDD, DDE), polychlorinated biphenyls (PCB's) and mercury in livers, but these levels declined over the period. N populations greatly reduced in hard winters, and total of 16 pairs on 32 km of R Thames, in England, was reduced to a single pair by severe winter of 1962/63; in most areas recovery is rapid, but may be hindered by pollution in some places. Locally is persecuted by humans to protect fish stocks.

**Bibliography.** Abdulali (1972b), Adamian & Klem (1999), Alexander (1992), Ali (1969, 1996), Ali & Ripley (1983), Allouze (1953), Amstutz (1973), Ancelet (1991), Anselin (1996), van Balen & van Balen (1993), Ballarín & Dominguez (1982), Bannerman & Bannerman (1971), Beaman & Madge (1998), Beaman *et al.* (1975), Beehler *et al.* (1986), van Bemmelen (1951), Bennett (1965), Boag (1982), Bosselmann & Esper (1985), Bottin *et al.* (1981), Brazil (1991), Bunzel (1987), Bunzel & Druke (1986, 1989), Burton (1978b), Butler (1990), Choffat (1992), Clancey (1935, 1936, 1992), Coates (1985), Coates & Bishop (1997), Collingie (1921), Cramp (1985), Cunningham (1970), Dagner (1997), Deignan (1945), Dementiev & Gladkov (1951), Diaz *et al.* (1996), Dickinson *et al.* (1991), Dodsworth (1912), Doucet (1969, 1971), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dupont (1984), Eastman (1969), Emde (1986), Énard & Étiévé (1970), Étiévé & Hùe (1964, 1978), Evans, M.I. (1994), Finch (1978a, 1978b, 1981a), Finger (1995), Fiorati (1992), Flint *et al.* (1984), Frost (1978), Fry (1994a), Fry *et al.* (1988), Garrod (1989), Gaumlett (1972), Gentz (1940), Gibson-Hill (1948), Glutz von Blotzheim & Bauer (1980), Goodfellow & Dare (1955), Goodman *et al.* (1989), Goto *et al.* (1997), Graf (1978), Gregory-Smith (1996, 1997), Grimmett *et al.* (1998), Gurevitch *et al.* (1978), Hagemeijer & Blair (1997), Haller (1977, 1978a, 1978b, 1982), Haller & Doucet (1982), Hallet-Libois (1984, 1985), Harper (1985a, 1985b), Harrison (1999), Harrop (1990), Hartmann (1977), Hassler (1983), Haupt (1987), Helbig (1978, 1987), Heyn (1963, 1965), Hirschfeld (1995), Hladik & Kadlec (1964), Hockey (1997), Hodson (1961), Hollick (1973), Hoogerwerf (1948b), Hornbuckle (1977), Hùe & Étiévé (1970), Ishikawa & Kudo (1998), Isotti & Consiglio (1995), Jayawardene (1989), Jeyarajasingam & Pearson (1999), Keller *et al.* (1989), Kennedy *et al.* (2000), Kniprath (1965, 1969a, 1969b), Konrad (1985), Krusk *et al.* (1993), Kuhl (1983), Kumari (1939a, 1939b, 1978), La Personne (1933), Laske & Helbig (1986), Ledant *et al.* (1981), Lekagul & Round (1991), Li Guiyuan *et al.* (1976), Libois (1987, 1993, 1994), Libois & Hallet-Libois (1985, 1989, 1999), Lambert (1991), Lincin & Libois (1994), Long *et al.* (1992), MacKinnon & Phillips (1993), Mackworth-Præd & Grant (1957), Madoc (1976), Marchant *et al.* (1990), van Marle & Voous (1988), Martin & Ibarra (1996), Martin & Pérez (1990), Massy (1983), McClure (1998), Meadows (1972a, 1972b, 1994), Meininger *et al.* (1978), Morgan & Glue (1977), Mozer (1987), Mukherjee (1995), Nishimura (1979), Numerov & Kotyukov (1979), Olsson (1993), Patil & More (1993), Paz (1987), Peeters (1978), Peris & Rodriguez (1996, 1997), duPont & Rabot (1973a), Porter *et al.* (1996), Pring-Mill (1974), Pris & Rodriguez (1996), Probst (1982), Proschl (1992), Purroy (1997), Puschmann (1976), Rabot (1977), Radetzky (1976), Raven (1986), Reichhoff (1979, 1988), Reinsch (1968), Rewcastle *et al.* (1997), Reynolds & Hinge (1996), Riviere (1933), Roberts (1991), Rogacheva (1992), Ruthke (1968), Rutledge (1968), Salomonsen (1934), Sayako *et al.* (1991), Schmidt, H.W. (1981), Schmidt, J. (1992), Schoenfeld (1997), Schulz-Waldmann & Dominiak (1971), Schumperlin (1991), Shirhan (1996), Shooter (1978), Smith (1969), Smythies (1986, 1999), Snow (1978), Snow & Perrins (1998), Stepanyan (1990, 1995), Taylor (1998), Tikader (1984), Tyler & Ormerod (1991), Wells (1999), Werner (1982), White & Bruce (1986), Wink & Gerstberger (1977), Yeatman-Berthelot & Jarry (1994), Zhao Zhengjie (1995), Zöller (1975, 1980).

## 82. Half-collared Kingfisher

### *Alcedo semitorquata*

**French:** Martin-pêcheur à demi-collier

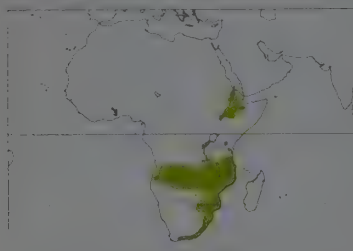
**Spanish:** Martin Pescador Cobalto

**German:** Kobalteisvogel

**Taxonomy.** *Alcedo semitorquata* Swainson, 1823. Great Fish River, South Africa. Forms a superspecies with *A. athis*, and formerly considered conspecific. Several races have been described, including *tephra* (equator to R Save in Mozambique) and *heuglini* (Dire Daoua in

Ethiopia), but regional variations in wing length and bill depth are slight and seem insufficient to warrant racial separation. Monotypic.

**Distribution.** Ethiopia and adjacent SE Sudan, and from Angola (Mossamedes) E to Tanzania and S to NE Namibia, E Botswana and NE & S South Africa; rare breeding records from Kenya.



**Descriptive notes.** 18 cm; 35-40 g. Male black lores with small buff line above, bright cobalt-blue head banded with black, particularly rich blue on ear-coverts and hindneck, white neckstripe; mantle to rump bright cobalt-blue, tail dark blue, scapulars and wing bright blue with green tinge; chin and throat white, deep blue half-collar on side of breast, remaining underparts buffy; bill black; iris dark brown; legs and feet vermillion-red. Female like male, but some red at base of lower mandible. Juvenile duller, paler, grey mottling on breast, blackish legs and feet. **VOICE.** High-pitched "tseep" given in flight, and "sip-ip-ip-peep"

in alarm; song ■ thin "tsip-tsip-tsiueep-tseep, tsiueep-tseueep-seep..."

**Habitat.** Slow-flowing channels through reedbeds, woodland streams, fast-flowing perennial rivers and streams with well-wooded banks and emergent vegetation; also reedy lakeshores, wooded coastal lagoons and estuaries and seashore in the E Cape. Mainly in lowlands, but to 2200 m in Ethiopia.

**Food and Feeding.** Small fish (*Alestes*, *Tilapia*, *Barbus*) 3-7 cm long, also crabs, frogs, aquatic insects and larvae (Odonata). Perches low on a branch, stump or rock over water, and dives in steeply to catch prey; returns with fish held head forwards in bill to perch, where prey beaten and then swallowed. Occasionally hovers briefly to scan for prey, and recorded taking a butterfly in flight. On R Sabie, in South Africa, prefers to forage in shallow water, but foraging success was not correlated with water depth; most perches were below 2 m, and below 1.5 m it used rocks and reeds almost equally, but above 1.5 m mainly branches.

**Breeding.** Lays in Jan-May, mainly Oct, in Tanzania; in Feb-Mar, Jun and Aug-Oct in Zambia; in Jul-Mar, mainly Sept-Oct, in Zimbabwe, and Sept-Mar in South Africa; 2 broods in Tanzania, and probably elsewhere. Nest in river bank, 40-130 cm from top, and 0-15-3 m from bottom of the bank or from water level; burrow 40-60 cm long, 5-7 cm in diameter, nest-chamber lined with fish bones. Clutch 2-6 eggs, mean 3.5; incubation by both sexes, sitting for 1-2 hours at a time, incubation period over 16 days; daytime brooding ceases after 5 days; both parents feed the young, visiting every 32 minutes on average, from 06:00 to 17:30 hours, with lull in activity 09:00-11:00 hours; nestling eats 50 g a day, parents later reduce feeding to encourage young to leave nest; nestling period c. 27 days; young leave nest soon after sunrise, follow an adult, some young fall into water and die.

**Movements.** Mainly resident, but some seasonal movements; Feb-Aug visitor to Begemdir and Simien Provinces of Ethiopia, and in South Africa more common in austral summer than in winter at Rondevlei and recorded from Kruger National Park only in wet summers. Records of a few vagrants in C Kenya.

**Status and Conservation.** Not globally threatened. Widespread, in a range of habitats, and locally common. Requires at least 1 km of river territory when breeding. Has declined on the Natal coast of South Africa as a result of pollution, river siltation and habitat loss.

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## 83. Blyth's Kingfisher

### *Alcedo hercules*

**French:** Martin-pêcheur de Blyth

**German:** Herkuleseisvogel

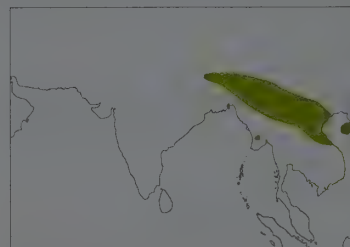
**Spanish:** Martín Pescador Hércules

**Other common names:** Great Blue Kingfisher

**Taxonomy.** *Alcedo hercules* Laubmann, 1917, Darjeeling.

Closely related to *A. atthis*. Sometimes referred to as *A. grandis*, but this name is preoccupied and therefore invalid. Monotypic.

**Distribution.** E Nepal E to Myanmar and S China (Yunnan, Hainan) and S to Laos and C Vietnam.



**Descriptive notes.** 22 cm. Male head feathers black with glossy bright blue tips, black lore with buffy streak above, buffy-white neck patch; mantle to uppertail-coverts brilliant cobalt-blue, with purple wash to rump and uppertail-coverts; tail dark ultramarine-blue; scapulars and wings blackish-green, upperwing-coverts tipped with cobalt; chin and throat buff-white, large blackish-blue breast patch, rest of underparts rufous; bill black; iris reddish-brown; legs and feet red. Female red base of lower mandible. Juvenile plumage not described. **VOICE.** In flight "psset", louder and less shrill than that of *A. atthis*.

**Habitat.** Streams and small rivers in deep ravines, hilly country and evergreen forest; also possibly on forest streams bordering well-wooded farmland. Occurs from 200 m to 1200 m, mainly 400-1000 m.

**Food and Feeding.** Mainly fish, but insect remains found in nest-burrows. From low, concealed perch in bushes overhanging water, it dives in for a fish and returns with it to perch. Some perches used repeatedly.

**Breeding.** Lays in Mar-Jun, mainly Apr-May, in NE India. Nest in bank of forest stream or vertical face of forest ravine; tunnel straight, initially inclining and then declining to nest-chamber, tunnel 8 cm wide, 45-60 cm long in hard earth but 200 cm long in sandy soil, with chamber 15-20 cm wide and 10-13 cm high. Clutch 4-6 eggs; both sexes incubate, and sit very tight; nest becomes foul with faeces and decaying food remains; no information on incubation and fledging periods.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Previously considered Vulnerable. Recent reports from much of its range, but in low densities. Total population probably rather small. Difficult to observe, because it is shy and timid. Probably only a vagrant in E Nepal; until recently considered rare in Bhutan, but regularly recorded in late 1990's; rare in NE India, and only a vagrant in Bangladesh; scarce to fairly common in Myanmar, and considered very rare (and possibly only a visitor) in NW Thailand; uncommon to locally common in N Laos and in Annamite Mts, but scarce farther S, and in Vietnam locally fairly common in W Tonkin and Annam; status in S China uncertain, but occurs in Mengyang Nature Reserve in S Yunnan and known to be present on Hainan. Could be threatened by deforestation, and possibly by human disturbance and water pollution. More information on its status and biology is required.

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From the ...  
The ...  
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PLATE 20

PLATE 20

Family ALCEDINIDAE (KINGFISHERS)  
SPECIES ACCOUNTS

Subfamily CERYLINAЕ

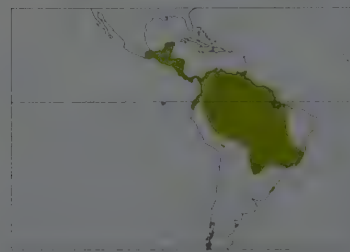
Genus *CHLOROCERYLE* Kaup, 1848

84. American Pygmy-kingfisher  
*Chloroceryle aenea*

French: Martin-pêcheur nain German: Erzfischer Spanish: Martin Pescador Enano  
Other common names: Pygmy/Least Green Kingfisher

**Taxonomy** *Alcedo aenea* Pallas, 1764, Surinam.  
Closely related to *C. inda*. Two subspecies recognized.  
**Subspecies and Distribution**  
*C. a. stictoptera* (Ridgway, 1884) - S Mexico (Puebla, Veracruz, Yucatán) to N & C Costa Rica.

*C. a. aenea* (Pallas, 1764) - C Costa Rica to N Colombia, S on W of Andes to W Ecuador, and on E of Andes E to Venezuela, the Guianas and Trinidad and S to E Ecuador, E Peru, N Bolivia, Paraguay, N Argentina (Misiones) and SC Brazil.



**Descriptive notes.** 13 cm; male 10-16 g, female 12-16 g. Male nominate race black lore with narrow rufous supraloral line, narrow rufous collar; dark glossy green head and upperparts with golden wash, tail bluer green, golden spots and tips on upperwing-coverts; chin and throat rufous, deeper on breast and flanks, centre of belly and undertail-coverts white; bill black, pale yellow base of lower mandible; iris dark brown; legs and feet fleshy to dark grey. Differs from very similar *C. inda* in much smaller size, white belly. Female has dark green breastband with white tips of feathers. Juvenile paler and duller underparts, buffy spots on wing, male green-black streaks on breast and flanks, female narrow often broken breastband.

spots on wing, male green-black streaks on breast and flanks, female narrow often broken breastband.



Race *stictoptera* 3-4 obvious lines of small white spots on secondaries (reduced and less white in nominate), and larger amount of white hidden in rump feathers. Voice. Weak, repeated "tik" or "dzit, tswek" sometimes faster as a rattle or chatter; song may be a series of musical chirps.

**Habitat.** Small streams, rivers and pools with dense overhanging marginal vegetation, in dense gallery forest and rainforest, ditches in plantations, open water in swamps, tidal channels in mangrove thickets; most common in shaded habitats, only 2-5% of observations in Colombia and Bolivia were from open shorelines. From sea-level to 2600 m.

**Food and Feeding.** Small fish (Characidae, Cyprinodontidae), tadpoles, also insects such as damselflies (Zygoptera). Perches low over water, frequently bobbing head and pumping tail, and catches prey by diving steeply into deep water, splashing in shallower water. Several reports of catching insects on the wing, but this may sometimes be mistaken interpretation of abortive sortie for fish. Frequently changes its foraging position. Detailed study in Colombia and Bolivia showed preferred perches were in trees, shielded by foliage (30%) and snags with only 1 or 2 prominent bare branches (29%); mean perch height was 1.2 m, and preferred prey was characid fish (96%), 30-70 mm long, most often 20-30 mm long.

**Breeding.** Lays in Mar-Apr, possibly Jun, in Costa Rica; in May in El Salvador and Surinam; in May-Sept in Trinidad; specimens in breeding condition in Jan in SE Mexico, in Aug in N Guatemala and in May in Belize. Nest in a riverbank, earth heap, gravel pit, cutting, arboreal termitarium or earth pulled up by an uprooted tree; may be some distance from water; nest-tunnel 30-40 cm long, dug by both of pair. Clutch 3-4 eggs. No other information.

**Movements.** Presumably sedentary.

**Status and Conservation.** Not globally threatened. Widely distributed; uncommon and local in some localities, but common in others. In Colombia and Bolivia densities varied, 0.9-1.4/km of shoreline at lakes and 0.3-1/km at streams.

**Bibliography.** Anon. (1998d), Belcher & Smooker (1936), Binford (1989), Blake (1953), Brace *et al.* (1997), Canevari *et al.* (1991), Castellino (1990), Chapman (1926), Chebez (1994), Cohn-Haft *et al.* (1997), Dickey & van Rossem (1938), Edwards (1989), Fjeldså & Krabbe (1990), Friedmann (1948), Haffer (1975), Haverschmidt & Mees (1994), Hayes (1995), Hayes *et al.* (1990), Herklots (1961), Hilty & Brown (1986), Howell & Webb (1995), Junge & Mees (1958), Lowen, Clay *et al.* (1997), Lowery & Dalquest (1951), Madroño & Esquivel (1997), Mazar *et al.* (1997), Meyer de Schauensee (1964), Meyer de Schauensee & Phelps (1978), Mitchell (1957), Monroe (1968), Novaes (1974), O'Neill & Pearson (1974), Paynter (1955), Pearson (1972, 1975a), Remsen (1979, 1986, 1990), Reynaud (1998), Ridgely & Gwynne (1989), Robinson (1997), Ruschi (1979), Russell (1964), Saibene *et al.* (1996), Sick (1993), Slud (1964), Smithe (1966), Smithe & Paynter (1963), Snyder (1966), Stiles & Skutch (1989), Stotz *et al.* (1996), Thurber *et al.* (1987), Tostain *et al.* (1992), Wetmore (1968), Willard (1985), Williams (1996), Williams & White (1997), Willis (1980), Willis & Eisenmann (1979), Winker *et al.* (1999).

## 85. Green-and-rufous Kingfisher

### *Chloroceryle inda*

**French:** Martin-pêcheur bicolore

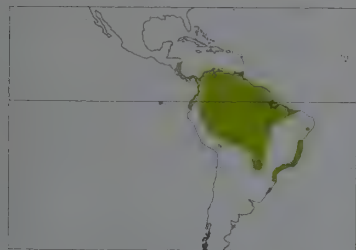
**Spanish:** Martin Pescador Verdirrufó

**German:** Zweifarbenfischer

**Taxonomy.** *Alcedo inda* Linnaeus, 1766, West Indies; error = Guiana.

Closely related to *C. aenea*. Birds from W Colombia and W Ecuador described as race *chocoensis* on basis of amount of buff spotting on wing-coverts and tail, but this character seems too variable to be useful for subspecific differentiation. Monotypic.

**Distribution.** SE Nicaragua and E Costa Rica to Colombia, W of Andes S to W Ecuador, and E of Andes across N half of South America, including Trinidad and Tobago, S to N Bolivia, E Paraguay and near coast of S Brazil.



**Descriptive notes.** 24 cm; male 40-60 g, female 53-62 g. Adult male dark glossy green above, apart from narrow rufous line above lore, and pale yellowish collar; upwing-coverts tipped with white, secondaries, tertials and tail with white spots; chin pale yellow-buff grading to buff-rufous on throat, remaining underparts rich dark rufous; paler underwing-coverts and undertail-coverts; bill black, pale yellow under lower mandible; iris dark brown; legs and feet fleshy to dark grey. Female like male, but broad breastband of white feathers with green tips, and more obvious pale spotting on forehead, wing-coverts, back and rump.

Juvenile like female, but more conspicuous spotting of wing-coverts, back, rump and uppertail-coverts; juvenile male also narrow breastband like female. Voice. Fairly quiet "chip-chip-chip", hard, rolling "drrrr", crackling "trit-trit-trit", and twitter followed by rapidly repeated, low "too-too-too-too"; song thin, high-pitched notes, "week week week".

**Habitat.** Streams and rivers with densely vegetated banks in forest, forested swamps and mangroves; most common in shaded habitats, only 6% of observations in Colombia and Bolivia were from open shorelines. From coast to 400 m.

**Food and Feeding.** Fish (Characidae, Cichlidae, Cyprinodontidae), crabs, shrimps (Palaemonoida), and aquatic insects. Sits on a low branch overhanging water, scanning for prey, with head bobbing and tail flicking; dives steeply into water and returns to perch with prey. Detailed study in Colombia and Bolivia showed preferred perches were in trees shielded by foliage (24%) and snags with only 1 or 2 prominent bare branches (21%); mean perch height was 1.67 m (but 5 m in Peru), and preferred prey was characid fish 30-70 mm long (77%) and shrimps (13%).

**Breeding.** Lays in Jul-Nov in N Brazil, possibly in Feb in NE Panama. Nest-tunnel dug into stream bank. Clutch 3-5 eggs. No other information.

**Movements.** Presumably sedentary, but disperses locally into flooded areas.

**Status and Conservation.** Not globally threatened. Widely distributed, and uncommon and local in some localities, but common in others. In Colombia and Bolivia variable densities: 1.7-2/km of shoreline at lakes, 1.4-3.8/km at streams and 0.2/km on larger rivers.

**Bibliography.** Aleixo & Galetti (1997), Anderson *et al.* (1998), Anon. (1998d), Brace *et al.* (1997), Brooks *et al.* (1993), Cohn-Haft *et al.* (1997), Cook (1996), Davis (1997), Friedmann (1948), Haverschmidt & Mees (1994), Hayes (1995), Hilty & Brown (1986), Lowen, Barnett *et al.* (1997), Madroño & Esquivel (1997), Mazar & Kirwan (1999), Mazar *et al.* (1997), Meyer de Schauensee (1964), Meyer de Schauensee & Phelps (1978), Novaes (1974), O'Neill & Pearson (1974), Pearson (1972, 1975a), Remsen (1979, 1986, 1990), Ridgely & Gwynne (1989), Robinson (1997), Ruschi (1979), Schönwetter (1966), Schubart *et al.* (1965), Sick (1993), Slud (1960, 1964), Snyder (1966),

Stiles & Skutch (1989), Stotz *et al.* (1996), Tostain *et al.* (1992), Wetmore (1968), Willard (1985), Willard *et al.* (1991), Williams (1996), Willis (1980), Willis & Eisenmann (1979).

## 86. Green Kingfisher

### *Chloroceryle americana*

**French:** Martin-pêcheur vert

**German:** Grünfischer

**Spanish:** Martin Pescador Verde

**Taxonomy.** *Alcedo americana* J. F. Gmelin, 1788, Cayenne.

Closely related to *C. amazona*. Other described races are *isthmica* (Honduras to E Panama, Pearl Is and N Colombia), *hellmayri* (W Colombia), *ecuadorensis* (Ecuador) and *crota* (Trinidad and Tobago), but all are poorly distinguished. Five subspecies recognized.

**Subspecies and Distribution.**

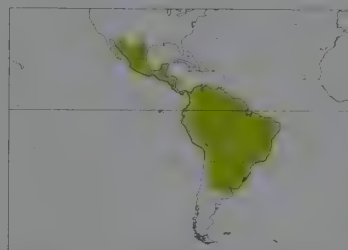
*C. a. hachisukai* Laubmann, 1942 - extreme S Arizona, SW New Mexico and WC Texas to NW Mexico.

*C. a. septentrionalis* (Sharpe, 1892) - SC Texas S to Colombia and W Venezuela.

*C. a. cabanisii* (Tschudi, 1846) - W Colombia and W Ecuador S on W of Andes to N Chile.

*C. a. americana* (J. F. Gmelin, 1788) - E of Andes from Venezuela and Trinidad and Tobago S to NE Bolivia and across N Brazil (Rondônia, Amazonas, Pará, Bahia).

*C. a. mathewii* Laubmann, 1927 - S Brazil and S Bolivia to N Argentina (Mendoza, N Buenos Aires).



**Descriptive notes.** 20 cm; male 29-40 g, female 33-55 g. Adult male black lores, white collar; remaining upperparts dark green with bronze reflections on crown; white spots on primaries, secondaries and wing-coverts form lines on wing; white spots on inner webs of tail feathers, and larger white patches on basal half of outer tail feathers; chin and throat white, breast bright rufous, belly white in centre with broad black-green bars on sides and flanks; undertail-coverts barred dark green and white; bill black, pale yellow at base of lower mandible; iris dark brown; legs and feet greyish. Differs from similar *C.*

*amazona* in much smaller size, distinct white spotting on wings, more white on sides of tail. Adult female like male, but has creamy-white throat and lower breast, upper breast glossy golden-green with white feather tips. Juvenile like female, but duller, less bronzy, with buff spots on crown and wing-coverts. Race *mathewii* smaller than nominate, lighter green upperparts, female less pronounced breastband; *hachisukai* longer bill, yellow-bronze wash over greens, more heavily spotted wing-coverts, secondaries and tail; *septentrionalis* longer wing and bill, less green on flanks and undertail-coverts, larger white spots on wing and tail; *cabanisii* longer wing, bill and tail, large white spots in secondaries, undertail-coverts white in Peru and green-spotted in Ecuador. Voice. Dry rasping, often followed by sputter, "dzeew dzeew kuk-kuk-kuk dzeew"; clicking sound "tick tick tick"; twittering rattle when alarmed; also creaking scratchy notes.

**Habitat.** Streams in woodland, muddy puddles in riverbeds, rocky watercourses, deep turbid rivers, pools in evergreen forest, flooded forest, lakes, marshes, choked drainage channels, coastal lagoons, mangroves, rocky coasts and coastal ports. Most common in open habitats; 58-94% of observations in Colombia and Bolivia were from open shorelines, and 3-31% from pools slightly separated from the main waterbody. From sea-level to 2800 m in Mexico, but more common below 1000 m.

**Food and Feeding.** Small fish (Characidae), crustaceans, prawns (Palaemonidae, *Penaeus aztecus*), also insects including dragonfly nymphs (Odonata), bugs (Hemiptera), ants (Hymenoptera). Searches for prey from waterside perch, rock or fence, occasionally bobbing head and flicking tail, then dives steeply into water and returns to perch with prey; occasionally hovers briefly 4-6 m above the water, scanning for prey. In Costa Rica, 50% of attacks were followed by a change in location before the next dive. Only 30% of dives are successful. Detailed study in Colombia and Bolivia showed preferred perches were in snags with only 1 or 2 prominent bare branches (52-56%) and in leafless trees (12%), sparsely (7%) or densely foliated trees (4-7%) and leafy (6-9%) or leafless bushes (9-15%); mean perch height was 1.5 m, and preferred prey was characid fish (88%) ranging in length up to 70 mm, most commonly 30-60 mm long when *C. inda* and *C. aenea* were present, and 10-20 mm in their absence; a species of shrimp made up 11% of the diet.

**Breeding.** Lays in Apr in Texas; in Mar, probably Jan-May, in Mexico; in Feb-Apr in Costa Rica; in Nov-Feb in Panama; in May-Aug and Dec in Surinam; and in Nov in Argentina. Nest in steep riverside or earth bank, 1-3 m above water level and often partially hidden by vegetation; both sexes excavate, tunnel 4-6 cm wide, 37-100 cm long, inclines to an unlined nest-chamber. Clutch 3-6 eggs, usually 4-5; female incubates at night, alternates with male during day, incubation period at least 21 days; chicks fed by both parents, leave nest c. 27 days after hatching, become independent 4 weeks later.

**Movements.** Sedentary.

**Status and Conservation.** Not globally threatened. Widespread, utilizing many habitats, and frequently common. In Colombia and Bolivia, densities found to vary: 0.4-3.7/km of shoreline at lakes, 0.7-5.6/km at streams, and 0.1-0.2/km at larger rivers.

**Bibliography.** Anon. (1998d), Araya & Chester (1993), Avelledo & Pérez (1994), Baicich & Harrison (1997), Belton (1984), Bent (1940), Betts & Betts (1977), Binford (1989), Bjelland & Ray (1977), Blake (1953), Brace *et al.* (1997), Brooks *et al.* (1993), Canevari *et al.* (1991), Chapman (1926), Chikilian & Bec de Speri (1968), Cohn-Haft *et al.* (1997), Contreras *et al.* (1990), Di Giacomo & López (2000), Dickey & van Rossem (1938), Edwards (1989), Fjeldså & Krabbe (1990), Fjeldså & Mayer (1996), Foster (1975), Gehlbach *et al.* (1976), Haverschmidt & Mees (1994), Hayes (1995), Herklots (1961), Hilty & Brown (1986), Howell & Webb (1995), Johnson (1967), Kaufman (1996), Klimatis & Moschione (1987), Lowery & Dalquest (1951), Mayr & Short (1970), Meyer de Schauensee (1964), Meyer de Schauensee & Phelps (1978), Mitchell (1957), Monroe (1968), O'Neill & Pearson (1974), Parker & Goerck (1997), Passmore & Thompson (1951), Paynter (1955), Pearson (1972, 1975a), de la Peña (1994), Pereyra (1932), Remsen (1979, 1983, 1986, 1990), Ridgely & Gwynne (1989), Robinson (1997), Root (1988), Ruschi (1979), Russell (1964), Schallbach (1963), Scharringa (1974), Schubart *et al.* (1965), Short (1974, 1975), Sick (1993), Skutch (1983), Slud (1964), Stiles & Skutch (1989), Stokes & Stokes (1996a, 1996b), Stotz *et al.* (1996), Urban (1959), Warner (1952), Wetmore (1926, 1957, 1968), Willard (1985), Willis (1980), Willis & Eisenmann (1979), Zimmer (1930).

## 87. Amazon Kingfisher

### *Chloroceryle amazona*

**French:** Martin-pêcheur d'Amazonie

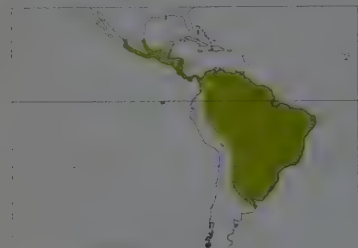
**Spanish:** Martin Pescador Amazónico

**German:** Amazonasfischer

**Taxonomy.** *Alcedo amazona* Latham, 1790, Cayenne.

Closely related to *C. americana*. N populations sometimes recognized as race *mexicana* on basis of larger size and slight plumage differences, but variation is clinal. Monotypic.

**Distribution.** Mexico and Belize S to Colombia and Venezuela, S on E of Andes to C Argentina (Buenos Aires, La Rioja).



**Descriptive notes.** 30 cm; male 98-120 g, female 125-140 g. Adult male dark bronzy green upperparts except for white collar and small white marks in front of and below eye (no white spot before eye in N populations); chin and throat white, separated from collar by narrow dark green line; breast rich rufous with dark green sides, belly white, flanks streaked with dark green; bill black, pale yellow under lower mandible; iris dark brown; legs and feet dark grey. Adult female like male, but white breast with bottle-green sides almost meeting in mid-line. Juvenile like female, but buff spots on upperwing-coverts, large yellow patch on

bill, male rufous-buff breast. **Voice.** Loud, harsh, repeated "tek" or "klek", staccato "chrit", given alone or rapidly repeated to become a rattle; also frog-like calls; greeting call or song or alarm to young an accelerating series of clear notes, rising in pitch, then decelerating and falling, "see see...su su su su".

**Habitat.** Large slow-flowing or fast-flowing rivers with rapids and deep pools, also lakeshores and wooded lagoons; occasionally brackish lagoons, winding channels in mangroves and tidal estuaries at coast. Most common in open habitats; 85-91% of observations in Colombia and Bolivia were from open shorelines, and 1-12% from pools slightly separated from main waterbody. Mainly below 1200 m, but to 2500 m in Venezuela.

**Food and Feeding.** Fish (Characidae), and crustaceans (*Penaeus aztecus*). Hunts from a perch, with occasional head-bobbing or tail-jerking, and dives into water for prey; on returning, beats the fish against perch before swallowing it head first. Occasionally hovers over open water, searching for prey, before diving down. Most hunting activity in morning and late afternoon, but may continue after sunset. Detailed study in Colombia and Bolivia showed preferred perches were in sparsely (31%) or densely foliated (28%) trees, on snags with only 1 or 2 prominent bare branches (19%), and on leafless trees (15%); mean perch height was 5-1 m, and preferred prey was characid fish (81%) in length range 10-170 mm, most commonly 60-70 mm long when *C. inda* and *C. aenea* were present, and 10-50 mm in their absence.

**Breeding.** Lays in Jan-Mar in Costa Rica, in Feb-May in Honduras and Panama, and in May in Trinidad; 1 brood. Male courtship-feeds female, raises his wings above back as greeting. Nest in riverbank, erosion gully or road cutting, usually near water; both of pair excavate, tunnel inclines slightly, straight or bending, 1-2-1-6 m long, 8-10 cm in diameter, ending in nest-chamber 25 cm wide, 45 cm long and 16 cm high; nests may be reused for several consecutive years, particularly if dug into rocky banks. Clutch 3-4 eggs, replacement laid if first clutch lost; incubation by female at night, mainly by male during day, period 22 days; chick's eyes start to open at 5 days, fully open 2-3 days later, body feathers emerge from sheaths at 12-13 days, well feathered and crest visible at 20 days; young fed by both parents; nest becomes foul with faeces and food remains, and may be infested with flies and maggots; adults often emerge backwards from tunnel and tumble into water to bathe after feeding; young fledge at 29-30 days.

**Movements.** Presumably sedentary, but occasional vagrants reported from Trinidad.

**Status and Conservation.** Not globally threatened. Widespread, and quite common in some localities. In Colombia and Bolivia, densities 0.95-5.6/km of shoreline at lakes, 0.8-4/km at streams, and 0.1-1/km at larger rivers.

**Bibliography.** Anon. (1998d), Belton (1984), Binford (1989), Brace *et al.* (1997), Brooks *et al.* (1993), Canevari *et al.* (1991), Castellanos (1932), Cohn-Haft *et al.* (1997), Contreras *et al.* (1990), Davis & Graham (1991), Dickey & van Rossem (1938), Edwards (1989), Fjeldså & Krabbe (1990), Haffer (1975), Haverschmidt & Mees (1994), Hayes (1995), Herklots (1961), Hilty & Brown (1986), Howell & Webb (1995), Klimaitis & Moschione (1987), Leck & Wilson (1970), Lowery & Dalquest (1951), Mayr & Short (1970), Meyer de Schauensee (1964), Meyer de Schauensee & Phelps (1978), Mitchell (1957), Monroe (1968), O'Neill & Pearson (1974), Paynter (1955), Pearson (1972, 1975a), de la Peña (1994), Remsen (1979, 1986, 1990), Ridgely & Gwynne (1989), Robinson (1997), Ruschi (1979), Saibene *et al.* (1996), Schaldach (1963), Schubart *et al.* (1965), Short (1975), Sick (1993), Skutch (1957, 1983), Slud (1964), Stager (1961), Stiles & Skutch (1989), Stotz *et al.* (1996), Thurber *et al.* (1987), Tomlinson (2000), Tostain *et al.* (1992), Wetmore (1926, 1968), Willard (1985), Willis (1980).





88

*ssp lugubris*

*ssp maxima*

*ssp guttulata*

*ssp gigantea*

89

*ssp torquata*

91

*ssp stellata*

90

*ssp travancoreensis*

92

*ssp rudis*



# Genus *MEGACERYLE* Kaup, 1848

## 88. Crested Kingfisher

### *Megaceryle lugubris*

**French:** Martin-pêcheur tacheté **German:** Trauerfischer **Spanish:** Martín Gigante Asiático  
**Other common names:** Great(er)/Large Pied Kingfisher

**Taxonomy.** *Alcedo lugubris* Temminck, 1834, Nagasaki, Japan.

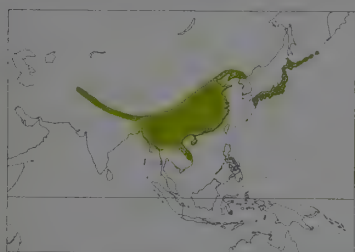
Genus sometimes merged into *Ceryle*. Forms a superspecies with *M. maxima*, *M. torquata* and *M. alcyon*. Proposed race *continentalis*, described from Sikkim, is poorly differentiated, and better merged with *guttulata*. Three subspecies currently recognized.

#### Subspecies and Distribution.

*M. l. guttulata* (Stejneger, 1892) - NE Afghanistan E through Kashmir, Nepal and NE India to Indochina, C, S and NE China, S to S Myanmar, NW Thailand and C Vietnam.

*M. l. pallida* (Momiya, 1927) - N Japan (Hokkaido), and possibly also S Kuril Is.

*M. l. lugubris* (Temminck, 1834) - C & S Japan (Honshu, Shikoku, Kyushu).



**Descriptive notes.** 41-43 cm; 230-280 g. Distinctive large kingfisher with long crest feathers. Adult male nominate race white loreal spot, long feathers on forehead and crown blackish-grey, spotted with white, when erect 2 patches of shorter white feathers; white-speckled black malar stripe, white collar; upperparts barred black and white, tail black with 6-8 white bars; white underparts, black-speckled breastband with rufous-orange feathers admixed, flanks barred with grey; bill black, basal half pale blue, tip yellowish; iris dark brown; legs and feet dark olive-grey. Adult female like male, but no rufous on breast, has bright pink-cinnamon underwing-coverts. Juvenile like female, but side of neck, breast, flanks and undertail-coverts washed with pale rufous. Race *guttulata* smaller than nominate (except in W Himalayas), darker upperparts and breast, larger but fewer white spots in crest, back and wings; *pallida* paler grey upperparts. **Voice.** Loud "ket ket" in flight, also loud "ping", deep croaks between paired birds, and raucous grating notes.

**Habitat.** Typical habitat is smaller, fast-flowing streams and rivers with rock or gravel base, in forested mountains and foothills; sometimes found at large rivers and river mouths; avoids rivers with bare open banks, but present along turbulent rapids. In Myanmar at up to 2800 m.

**Food and Feeding.** Fish 15-18 cm long, and crayfish. Perches on an overhanging branch, partly submerged log or rock, occasionally bobbing head, raising crest and flicking tail, then dives obliquely into water for a fish. Favoured stretches of river are fished repeatedly.

**Breeding.** Lays in Mar-Jun in Nepal, in Apr in China and in Apr-Jul in Japan. Territory of a single bird may be 4 km<sup>2</sup>. Nest-site a vertical bank, often sandy and at least 2 m high, by a stream, in a ravine or in forest, and can be 1.5 km from water; in Kyoto Prefecture (Japan), nests were usually in banks more than 2 m high, up to 1500 m from water and at least 1400 m apart; both sexes dig tunnel 2-3 m long and 10-15 cm wide, ending in a chamber 30-50 cm wide; in Kashmir, a pair dug 1 m of a tunnel in sandy soil in 20 hours; nest may be reused. Clutch 4-7 eggs, usually 4-5; apparently only female incubates, period not documented; both sexes feed the young, which fledge after c. 40 days.

**Movements.** Altitudinal migration in Japan and the Himalayas, with movement to lower country in winter to avoid frozen rivers, but some birds remain in winter around hot springs in the Kitami Hills, in Hokkaido. Elsewhere seems to be sedentary, with only local movements. Previously breeding in Hong Kong, but now considered a passage migrant there, recorded in all months (peak in Apr-May), probably resulting from altitudinal movements. Vagrant to Korea and E Manchuria.

**Status and Conservation.** Not globally threatened. Widespread and common in some areas, but numbers have declined sharply during 20th century in Hokkaido, and also in Hong Kong, where no longer breeds in Lam Tsun Valley. Deforestation and human disturbance are likely causes of population declines. In Kashmir, has sometimes been shot for preying on trout (*Salmo*).

**Bibliography.** Ali & Ripley (1983), Ali *et al.* (1996), Austin (1948), Austin & Kuroda (1953), Baker (1934a, 1934b), Bangs & Van Tyne (1931), Barker *et al.* (1999), Bates & Lowther (1952), Brazil (1991), Deignan (1945), Duckworth *et al.* (1999), Etchécopar & Hüc (1978), Gore & Pyong-Oh (1971), Grimmer *et al.* (1998), Harvey (1990), Inskipp & Inskipp (1991), Inskipp *et al.* (1999), Kazmierczak (2000), Kuroda (1991), Lekagol & Round (1991), MacKinnon & Philipps (2000), Meyer de Schauensee (1984), Muir (1916), Neehaev & Kurenkov (1987), Nishimura (1979), Riley (1938), Roberts (1991), Robson (2000a), Round (1988), Smythies (1986), Stepanyan (1990), Thewlis *et al.* (1998), Tomlinson (2000), Vieillard (1969), Webster (1975), Wildash (1968), Won (1993), Zhao Zhengjie (1995).

## 89. Giant Kingfisher

### *Megaceryle maxima*

**French:** Martin-pêcheur géant **German:** Riesenfischer **Spanish:** Martín Gigante Africano  
**Other common names:** African Giant/Aluean Giant Kingfisher

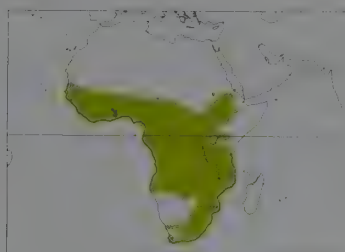
**Taxonomy.** *Alcedo maxima* Pallas, 1769, Cape of Good Hope.

Genus sometimes merged into *Ceryle*. Forms a superspecies with *M. lugubris*, *M. torquata* and *M. alcyon*. Validity of race *gigantea* has been questioned, since light and dark forms have been found together in Liberia and both the Upper and Lower Guinea forests; further investigation required. Two subspecies tentatively recognized.

#### Subspecies and Distribution.

*M. m. maxima* (Pallas, 1769) - open areas from Senegambia E to W Ethiopia and S to S Angola, N Botswana, and South Africa, mainly in E half, S to Cape Town and SW, and also Orange R.

*M. m. gigantea* (Swainson, 1837) - forest from Liberia to N Nigeria, then E to W Tanzania and S to N Angola.



**Descriptive notes.** 42-46 cm; male 275-426 g, female 255-398 g. Adult male of nominate race has black forehead, crown and hindneck with small white spots on crown, black lores and ear-coverts with small white loreal spot; back black with white spots, tail black with 6-8 narrow white bars; white chin and throat, black malar stripe, breast rich coppery brown, belly white with large irregular dusky bars; bill black; iris dark brown; legs and feet grey. Adult female like male, but breast black or densely spotted black, belly, flanks, undertail and underwing-coverts rich copper-brown. Juvenile male black speckles on side of breast, some

rufous on flanks, juvenile female less densely spotted on breast with some rufous fringing, white band between breast and belly. Race *gigantea* darker, less spotting on upperparts, heavier bars on underparts. **Voice.** Loud, raucous, cackling "kek" when disturbed, may be repeated as "kek-kek-kek-kek"; greeting call similar but softer, "kah, kah, kah", can also form a rattle, "keriririririri", one bird may give single call and the other a rattle; also loud sharp "kakli", and a "kee-ou, kee-ke-ou" in flight.

**Habitat.** Large perennial rivers, and dams and lakes with plenty of marginal woody growth, in forest and savanna regions; also coastal lagoons, mangroves, estuaries, rocky and sandy seashores, sometimes fishing up to 100 m from shore. Also occasionally on stagnant pools along dried-up rivers, on rapids, in flooded woodland, drainage channels and garden fish ponds. At up to 1600 m in Tanzania.

**Food and Feeding.** Mainly fish (Cichlidae, Serranidae) in Zaire and Zimbabwe, and river crabs (including *Potamon*) in Liberia and South Africa; also frogs, clawed toads (*Xenopus*), and occasionally centipedes (Chilopoda), small reptiles and insects. Newly fledged young are fed fish up to 18 cm long. Scans for prey from overhanging branch or sheltered rock: on R Sabie, in South Africa, most perches were on branches and 85% were over 4 m high. Dives in with a steep or shallow dive, usually immersing completely; occasionally hovers above open water. Small crabs are eaten whole; those with carapace over 30 mm in width are moved to the tip of the bill, then hit on perch with swinging movements to left and right until pincers and carapace are removed, before being swallowed. Fish usually swallowed head first, occasionally tail first. After a successful capture, it will fly to a new feeding perch, moving 2-5 times an hour and flying a total of 7-8 km a day. In South Africa, most active in morning, late afternoon and evening, which coincided with the activity patterns of the crabs. After fishing in the sea, it dives in fresh water to clean itself.

**Breeding.** Lays in Nov-Feb in Senegambia, in Mar in Mali, in Dec-Jan in Liberia, in Dec in Cameroon, in Jan-Mar in Zaire, in Aug in Ethiopia, in May-Oct in E Africa; in Mar-Apr and Jun-Aug (mainly Aug) in Zambia, in Aug-Mar (mainly Sept-Oct) in Zimbabwe, and in Sept-Jan in South Africa. Monogamous, solitary breeder. Nest located in bank of a river, cliff, sand quarry or dam spillway; in South Africa tunnels averaged c. 2.3 m (0.5-5 m) above foot of bank and 0.83 (0.3-1.5) m from top of bank, and up to 1.6 km from flowing water; entrance may be concealed behind overhanging vegetation; tunnel dug over 7 days by both sexes, using initially bill and then bill and feet to move loosened soil back; tunnel 9-15 cm wide, 11 cm high, on average c. 1.8 m long (0.9-8.5 m), nest-chamber 20-60 cm in diameter, unlined. Clutch 3-5 eggs (mean 3.5 in South Africa); both sexes incubate, with change-overs 3 or 4 times a day, period not documented; 2 chicks hatch together, the third 1-2 days later, mean brood size in South Africa 2.4 (range 1-4); male removed eggshells, dropped them on water and dived to sink them; at a nest with 2 young, a fish was brought every 150 minutes, at another with 3 young visits were every 108 minutes; chamber becomes foul with discarded food, pellets and faeces; 2 nestlings in E Zambia grew from 100 g at c. 4 days old to 300+ g at c. 14 days and length of upper mandible doubled from 16 to 32 mm, a third nestling was significantly smaller; eyes were completely open at 8 days; male stopped feeding on 30th day, female stopped on 35th day, and young flew on 37th day; fledglings started diving within a few hours, but female was still feeding them 3 weeks later.

**Movements.** Generally resident, with some local movements which may involve dispersing juveniles, or adults exploiting ephemeral pools. Nocturnal movements to isolated waterbodies some distance from daytime range have been reported, but none detected during a radio-tracking study in South Africa. Little indication of seasonal movement, but absent from NW Ethiopia in Oct-Dec and a dry-season visitor to Serti, in Nigeria.

**Status and Conservation.** Not globally threatened. Widespread, and common in some localities. A pair in South Africa had a home range of 4.3 km on a river. May suffer from pesticides draining into rivers from adjoining farmland. Regarded as a pest at some trout (*Salmo*) hatcheries.

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## 90. Ringed Kingfisher

### *Megaceryle torquata*

**French:** Martin-pêcheur à ventre roux **Spanish:** Martín Gigante Neotropical  
**German:** Rotbrustfischer

**Taxonomy.** *Alcedo torquata* Linnaeus, 1766, Mexico.

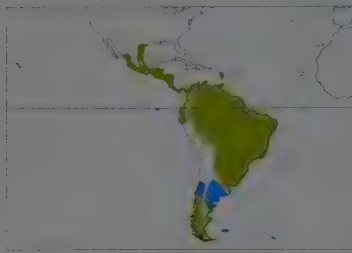
Genus sometimes merged into *Ceryle*. Forms a superspecies with *M. lugubris*, *M. maxima* and *M. alcyon*. Three subspecies recognized.

#### Subspecies and Distribution.

*M. t. torquata* (Linnaeus, 1766) - extreme S Texas and NW Mexico S to Peru, SE Bolivia, NE Argentina and Uruguay, also Margarita I (off N Venezuela) and Trinidad.



*M. t. stictipennis* (Lawrence, 1885) - Guadeloupe, Dominica, Martinique and Grenada, possibly also St Kitts.  
*M. t. stellata* (Meyen, 1834) - S Chile and Argentina to Tierra del Fuego; migrates N to C Chile and NE Argentina.



**Descriptive notes.** 40 cm; male 254-330 g, female 274-325. Adult male nominate race bluish slate-grey head, side of breast, mantle, back and uppertail-coverts; white frontal spot and semicircle below eye; broad white collar; primaries black, secondaries and wing-coverts blue-grey, feathers with white marks on inner webs; tail black with blue-grey edges and 5 pairs of white spots; breast to belly deep-rufous, undertail-coverts white with grey bars, underwing-coverts white; bill grey-black, paler at base and pale yellowish at base of lower mandible; iris dark brown; legs and feet grey. Adult female like male, but blue-grey band on

upper breast separated from rufous belly by narrow white band, deep rufous underwing-coverts and undertail-coverts. Juvenile like female, but streaky upperparts, paler underparts, rufous wash on grey breast, underwing-coverts partly white. Race *stictipennis* has white spots on secondaries extending onto outer webs; *stellata* like previous, but undertail-coverts more heavily marked with grey. **Voice.** Single loud "klek" is a contact call, or given in flight, may be repeated; alarm a rattling "klek-klek-klek-klek..."; pair-members alternate low chatters while waving tail.

**Habitat.** Large, slow rivers, lakes, reservoirs, marshes, estuaries, coastal lagoons, Chilean fiords, mangroves, rice fields, canals, water-gardens and open beaches; usually found in heavily wooded areas, but foraging up to 1 km offshore on reefs. Most common in open habitats; 87-99% of observations in Colombia and Bolivia were from open shorelines, and 0-5-10% from pools slightly separated from main waterbody. From sea-level to 1500 m in Guatemala, but generally uncommon above 500 m.

**Food and Feeding.** Mainly fish (Characidae, Cichlidae) to 20 cm in length, also frogs, salamanders (Urodela), reptiles, crabs and insects. Sits patiently on a perch overhanging water, occasionally raising crest or cocking tail; dives steeply into water for prey, returning with it to perch, where it is stunned by beating vigorously and then swallowed head first; may stay at same perch or fly to another favoured one. Sometimes hovers up to 15 m above water before diving down. Detailed study in Colombia and Bolivia showed preferred perches were in sparsely (34%) or densely (30%) foliated or leafless (29%) trees; mean perch height was 7-1 m, and preferred prey was characid (81%) or cichlid fish (12%); fish ranging in length from 20 mm to 180 mm, most commonly 80-110 mm.

**Breeding.** Lays in Mar in Texas, in Jan in Mexico, in Apr-May in Belize, in Mar-May in Panama, in Mar-Jul in Surinam, in Jul in Argentina, and in Oct-Nov in Chile; in Apr in Trinidad and in Aug in Guyana. Usually solitary breeder, but small colonies of 4-5 nests reported from R Orinoco, and exceptionally a colony of 150. Nest-site usually a riverbank or bank of lake, dam or lagoon, but erosion gully or road cutting far from water sometimes used; nest sometimes close to that of Torrent Duck (*Merganetta armata*); tunnel dug by both sexes, 10 cm high, 10-15 cm wide and 2-3 m long, ending in an enlarged chamber. Clutch 3-6 eggs, usually 4; both parents incubate, for 24 hours at a time, with change-over in the morning 07:00-10:00 hours, and with short (30 minutes) unrelieved break in afternoon; incubation period not less than 22 days; both parents feed the young; young have eyes open at 10 days, are feathered apart from abdomen at 24 days, and leave nest at c. 35 (33-38) days, flying strongly.

**Movements.** Mainly sedentary, but makes local movements overland to distant waterbodies, often in the early morning or evening. A breeding visitor Nov-Mar in S (Tierra del Fuego); post-breeding migration N to as far as Valparaíso, NE Argentina and Buenos Aires, with records from Trinidad in Mar-Jun.

**Status and Conservation.** Not globally threatened. Widespread, and plentiful in many localities. In Colombia and Bolivia, densities of 0.24-5.6/km of shoreline at lakes, 0.7-5.2/km at streams, and 0.2-2.7/km at larger rivers.

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## 91. Belted Kingfisher

### *Megasceryle alcyon*

**French:** Martin-pêcheur d'Amérique

**Spanish:** Martin Gigante Norteamericano

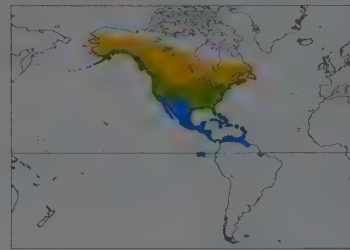
**German:** Gürtelfischer

**Taxonomy.** *Alcedo Alcyon* Linnaeus, 1758, South Carolina.

Genus sometimes merged into *Ceryle*. Forms a superspecies with *M. lugubris*, *M. maxima* and *M. torquata*. Proposed separation of population from W coast as race *caurina* on basis of larger size is unwarranted, as size is variable across species' entire range. Monotypic.

**Distribution.** Aleutian Is and CW Alaska (Seward Peninsula) E through C Canada to Labrador and Newfoundland, and S throughout USA to S California and S Texas and N coast of Gulf of Mexico. Winter range S to E Panama, N Colombia, Venezuela, Guyana, Galapagos Is and the Caribbean to Trinidad.

**Descriptive notes.** 28-33 cm; male 113-173 g, female 138-178 g. Adult male bluish-grey head with distinct crest; white frontal spot, very narrow semicircle under eye, broad collar around neck; upperparts, scapulars and wings blue-grey; white underparts, blue-grey breastband; underwing-coverts white; bill mostly blackish; iris dark brown; legs and feet grey. Adult female rufous sides to upper breast, rufous breastband on lower breast below grey breastband, rufous flanks. Juvenile like adult female, but rufous wash to grey breastband, stronger in juvenile female. **Voice.** Most common call the rattle, a loud, harsh "Kekity-kek-kek-kek-ik-ticky-kek", used in territorial disputes, when humans enter ter-



ritory and around conspecifics; scream given when retreating from a threat or approaching another bird; harsh call by male early in breeding season often indicating territorial aggression, quieter warble by female soliciting copulation or before courtship feeding; high-pitched squeaks, mew call, given in courtship-flight.

**Habitat.** Mountain streams, rivers, lakes, swamps, tidal creeks, coasts and garden ponds; needs clear, still water, not overgrown with vegetation, usually with elevated perches for fishing, but also recorded foraging offshore; stream riffles an important location of food,

and territories smaller where riffles common; availability of nest-sites may also be important for habitat selection. Uses similar habitats in winter range, but less frequently found around lakes and large rivers, and also utilizes mangroves and offshore islands. More tolerant of changing river levels than are other large kingfishers. From sea-level to 2500 m.

**Food and Feeding.** Mainly fish, up to 14 cm long (mean 9 cm); recorded genera include *Salvelinus*, *Cottus*, *Gasterosteus*, *Pungitius*, *Salmo*, *Campostoma*, also *Couesius*, *Catostomus*, *Notropis*, *Luxilus*, *Rhinichthys*, *Hybognathus*, *Pimephales*, *Fundulus*, *Hybopsis*, *Morone*, *Pomolobus*, *Perca*, *Nocomis*, and *Umbra*. Other foods include crustaceans (*Cambarus*), molluscs, frogs, salamanders (Urodela), lizards, young sparrows and quail (*Colinus*), water shrews (*Sorex*), dragonfly nymphs (Odonata), grasshoppers (Orthoptera), moths and butterflies (Lepidoptera); also berries in winter. Generally takes those fish that are most abundant, and are present in shallow water or swim near the surface; in Michigan, trout comprised 17% of the diet of birds on lakes, but 29-80% on trout streams. Pellets of indigestible remains are found below favourite roosting spots. Forages from a perch or by hovering up to 15 m above the water; dives obliquely or vertically into the water, spreading its wings to brake the dive under water. Fish usually caught less than 60 cm below surface, and typically does not submerge; fish is grabbed in the bill with a pincer-like action, held one-third of the length back, and taken back to the perch, where it is beaten before being swallowed whole. Invertebrates are sometimes dismembered while being beaten, but fallen legs or crayfish claws are not retrieved; crayfish swallowed tail first, with tail curled under the body. Swoops down to catch lizards and arthropods in dry, sandy riverbeds in Arizona. Reported following Great White Egrets and Snowy Egrets (*Egretta alba* and *E. thula*) and diving after fish disturbed by the egrets. A study in Colorado showed that most of time was spent perching (98.2-99.2%), and birds were most active in the afternoon (7-2 flights/h) and least active in the morning (4-1 flights/h), and made more successful dives in the afternoon, with an overall success rate of 84%. Calculated daily energy consumption was 230-254 KJ/day for 130-g captive adults, and estimated 264 KJ for wild 148-g birds. Forage up to 0-8.8 km from the nest, and has been seen fishing up to 1 km out to sea. Active from before sunrise to after dark (04:00-23:00 hours).

**Breeding.** Lays in Apr-Jun in Louisiana, in Apr-Jul in New York State, in May-Jun in Illinois, Massachusetts and Minnesota, in May-Jul in Ontario; food supplementation caused earlier nesting in Colorado; single brood. Female visits territory established by male, with noisy chasing flights; male courtship-feeds, copulation sometimes follows; often aerial display by pair soaring high and dipping close to the lake, then female perches and male continues spiral ascent ending in a stall and somersaulting descent, then rising glide with wings extended. Preferred nest-site a well-drained vertical bank near water, free of vegetation, alternatively earth cutting, ditch, road cutting, embankment, mound, gravel pit, mud-slide made by beavers (*Castor canadensis*), soil in roots of fallen tree, tree hole, sand dune or sawdust heap, sometimes far from water; important factors in selection of site were that bank was high, steep, with soil having high percentage of sand, although sites in a Colorado study were in less sandy soil than expected; both sexes dig tunnel, male does more, can be completed in a few days in sandy soil but up to 3 weeks in hard or rocky ground; nest-tunnel 1-2 m long (exceptionally to 5 m), 9 cm in diameter, inclining slightly, with a lip before the egg-chamber, chamber 20-30 cm in diameter and 15-18 cm high, not lined, but layer of broken pellets accumulates on floor during incubation. Clutch usually 6-7 eggs, range 5-8, mean 4-2 in Louisiana; reports of 11-14 eggs in clutch probably result from 2 females laying in same nest; eggs laid early in morning on consecutive days; replacement clutch may be laid, sometimes in new burrow, if first one lost; incubation starts with last egg, by both sexes, female remaining in nest overnight, incubation period 22-24 days; hatching usually synchronous, over 12-18 hours; hatching bright pink with black bill, no down, eyes open at c. 14 days. Feathers emerge from sheaths at 17-18 days; young brooded, mainly by female, continuously for first 3-4 days, brooding ceases after 6 days; both sexes feed young, for first 4 days on regurgitated, semi-digested fish, later mainly male brings whole fish in morning and early evening, estimated 8-3 fish/chick/day; nestling period 27-35 days; adults reduce feeding 3-4 days before young fledge, but feed them for 3 weeks after fledging; for several days after leaving nest juveniles perch nearby, and have weak flight. In Minnesota, hatching success was 87% and fledging success 97%.

**Movements.** A partial migrant in most of range, with birds moving S in winter to S USA and C America to Panama from Sept to early Apr, and West Indies to Trinidad from mid-Oct to late Apr. A summer visitor to Alaska, but some regularly overwinter on SW coast, and records of birds wintering throughout breeding range; males more likely than females to overwinter in breeding area; no breeding records from Bahamas but some birds regularly overwinter there; winter migrants establish individual territories. Early reports indicate that birds fly S on shores of L Michigan in autumn at rate of 12 per hour, and fly N on W shore of L Huron in spring at 15 per hour; migrants also common along Atlantic coast; offshore movement apparently rare, but some sightings are over 600 km from Atlantic coast. Some nocturnal migration may occur. Fledglings disperse locally within 1 month of leaving nest, and return in following year to the general area of their hatching. Vagrants reported from Hawaiian Is, Azores, Netherlands, Iceland, Greenland, Ireland and England.

**Status and Conservation.** Not globally threatened. Widespread, and common in some localities. Densities of 1 bird/160 m of farmland streams in New Brunswick, 1 pair/km<sup>2</sup> at L Itasca, in Minnesota, 1 pair/1.5 km of river in Colorado, and 1 nesting pair/2 km of shoreline in Ohio. Breeding territories were considerably larger (1030 m) than non-breeding territories (389 m) on a creek in Ohio. No significant trends in populations during 1965-1979, but decline of 1-1% annually over 1982-1992. Sensitive to human disturbance, particularly when breeding, but excavation of sand and gravel pits and other construction work has provided nesting sites, allowing population expansion in some areas. Pesticide pollution of waterways a potential threat to this species, but it seems more resistant to contaminants than do other piscivores; eggshell quality declined during the period of widespread use of DDT, but reproductive success was not greatly diminished. Although often identified as a major threat to fish hatcheries, its actual impact may be less than that of other, less conspicuous birds. Over 5000 were killed at fish farms in Michigan in 1937, and 400 were killed during one spring migration at a trout hatchery near L Michigan. Many hatcheries continue to use shooting and trapping, either under licence or illegally, to protect fish stocks.



**Bibliography.** Amos (1991), Anon. (1998d), Arendt (1992), Armstrong (1983), Baieich & Harrison (1997), Bailey (1907), Beaman & Madge (1998), Beatty (1999), Bendire (1895), Bent (1940), Berger (1981), Biaggi (1983), Binford (1989), Blake (1953), Brooks & Davis (1987), Brudenell-Bruce (1975), Bull (1974), Campbell *et al.* (1990), Carey (1909), Conner (1978), Cornwell (1963), Cramp (1985), Cyr (1995), Davis, W.J. (1980, 1982, 1985, 1986, 1988a, 1988b), DeGraaf & Rappole (1995), Droege (1987), Edwards (1989), Eipper (1956), Feilberg (1985), French (1966), Fox (1974), Gabrielson & Lincoln (1959), Godfrey (1986), Hamas (1974, 1975, 1981, 1991, 1994), Hamel (1976), Henshaw (1902), Herklots (1961), Hilty & Brown (1986), Hopkins (1980), Howell & Webb (1995), Hoyt (1961), Johnsgard (1979), Johnson (1925), Kaufman (1996), Kelly (1996, 1998a, 1998b), Kelly & Van Horne (1997), Kilham (1974), Kirby & Fuller (1978), Kiviat *et al.* (1985), Kustich (1997), Lincoln (1924), Mayr & Short (1970), McCabe & McCabe (1928), McKee (1981), Meyer de Schauensee (1964), Meyer de Schauensee & Phelps (1978), Meyerreicks & Nellis (1968), Mousley (1938), Mullarney (1981), Passmore & Thompson (1981), Phillips (1962), Pittaway (1994), Pratt *et al.* (1987), Price *et al.* (1995), Prose (1985), Raffaele *et al.* (1998), Rappole *et al.* (1995), Ridgely & Gwynne (1989), Root (1988), Russell (1964), Salyer & Lagler (1946), Schaldach (1963), Scott (1984), Sens (1999), Shields & Kelly (1997), Shufeldt (1884), Skinner (1928), Skutch (1945a), Slud (1964), Small (1994), Snook & Sullivan (1988), Snow & Perrins (1998), Stevenson (1919), Stiles & Skutch (1989), Stokes & Stokes (1996a, 1996b), Terres (1968), Torsey (1989), Urban (1959), Vessel (1978), Voous (1983), Weber & Miller (1981), Wetmore (1968), White (1936, 1937, 1938, 1939, 1953), Willis (1980), Wilson & Ceballos-Lascurain (1993).

## Genus *CERYLE* Boie, 1828

### 92. Pied Kingfisher

#### *Ceryle rudis*

**French:** Martin-pêcheur pie **German:** Graufischer **Spanish:** Martin Pescador Pio  
**Other common names:** Lesser/Small Pied Kingfisher; Indian Pied Kingfisher (*travancoreensis*, *leucomelanura*)

**Taxonomy.** *Alcedo rudis* Linnaeus, 1758, Egypt.

Distinctive, with no close relatives, although some authors have placed some or all members of *Megaceryle* in present genus. Four subspecies recognized.

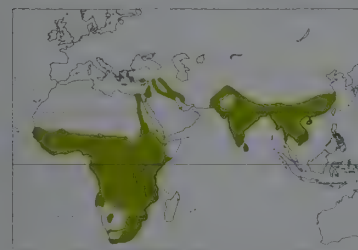
#### **Subspecies and Distribution.**

*C. r. rudis* (Linnaeus, 1758) - C & S Turkey and Israel to Syria, Iraq and SW Iran, also N Egypt and Nile Valley, and sub-Saharan Africa (except arid regions).

*C. r. leucomelanura* Reichenbach, 1851 - NE Afghanistan, W Pakistan and India (except SW) S to Sri Lanka, and E to Thailand and Indochina.

*C. r. travancoreensis* Whistler & Kinnear, 1935 - SW India, from N Kerala S to Cape Comorin.

*C. r. insignis* Hartert, 1910 - SE China, including Hainan.



**Descriptive notes.** 25 cm; male 68-100 g, female 71-110 g. Distinctive medium-sized kingfisher with black and white plumage. Male nominate race black crown and crest, white stripe above eye, black eyeband to hindneck, white throat and collar; black upperparts with white edgings, rump barred black and white, white patch on wing-coverts; white below with two black breastbands, the upper broad and often almost broken in middle, lower one narrower; bill almost entirely black; iris dark brown; legs and feet blackish. Adult female only single breastband, narrower and often broken in centre. Juvenile like female, but brown

fringe to feathers on lores, chin, throat and breast. Race *leucomelanura* blacker upperparts, black spots on flanks and side of throat; *insignis* like previous but longer bill; *travancoreensis* even blacker upperparts, more black spots on flanks and side of throat, longer bill. Voice. Alert call, frequently given in flight or from perch, "kwik-kwik" or "chirruk, chirruk"; alarm low-pitched "trrr trrr trrr"; distress call shrill, rapidly repeated "preepreepreepreep"; contact call, arriving or leaving nest or roost, "tréetiti, tréetiti"; advertising call, given in defence of nest-site or perch, high-pitched "chickkerker"; aggressive call shrill repeated "shreer"; appeasement "werk...werk. werk. werk. werk. werk. erk"; begging call brief repeated "pi-chee"; courtship-feeding calls soft warbled sounds and chirps; copulation call very soft "pirree".

**Habitat.** Small and large lakes, large rivers, estuaries, coastal lagoons, mangroves and sandy and rocky coasts, dams and reservoirs with either fresh or brackish water; also streams and smaller fast-flowing rivers, marshes and paddyfields, and even feeding from roadside ditches. Requires water-side perches such as trees, reeds, fences, posts, huts and other man-made objects; large papyrus swamps in Uganda and the centre of open floodplains in Zambia are avoided. From coast to 2500 m in Rwanda, coast to 1800 m in India.

**Food and Feeding.** Largely fish in Africa, including *Engraulicypris argenteus*, *Haplochromis*, *Barbus* and *Clarias* at L. Victoria; *Haplochromis*, other cichlids, *Barbus paludinosus* in Botswana; in South Africa, *Ambassis natalensis*, *Gilchristella aequatarius* and many other species in Kosi Estuary, and also *Sarotherodon mossambicus* at L. St Lucia; *Barbus*, *Alestes* and cichlid species in Zambia, and cichlids *Cyrtocara eucinostomus* and *Pseudotropheus zebra* in Malawi. Preferred size range of fish 25-60 mm, but those up to 133 mm and 26 g are taken. Aquatic insects may supplement this, and dragonfly nymphs (Anisoptera) were 24% of all prey items on Kafue Flats, in Zambia; also winged insects, e.g. adult dragonflies, alate termites (*Macrotermes*); and grasshoppers (*Ruspolia flavovirens*), water beetles (Dytiscidae, Gyrinidae), water scorpions (Nepidae), water-bugs (Notonectidae, Corixidae, Belostomatidae); 2 birds flushed from a carcass in Tanzania were probably feeding on maggots. In the Sundarbans of India, fish included *Mugil parva*, *Ambassis*, *Puntius* and *Mystus*, with crabs and crayfish (17% of prey) and aquatic insects (26%) also taken. Frogs, tadpoles and molluscs also recorded, though latter may be secondarily ingested. Average daily food intake estimated to be 18.4 g (24.6% of body weight), representing 7.2 fish/bird/day; 2 hand-reared juveniles near to fledging also had daily intake of 24-26% of body weight, but younger captive nestlings ate 34.5 g/day (45% of body weight). Pellets consisting of undigested bones and insect sclerites are produced at night and during resting

periods during day, prior to resuming foraging. Hunts by scanning from perch, bobbing head and flicking tail, and then diving down, hitting water with a splash, returning with prey carried crosswise in its bill. Small fish may be swallowed in flight; larger ones (over 55 mm) taken back to perch and bashed repeatedly, up to 113 times for a 9-cm *Tilapia*, before being swallowed head first. Also regularly hovers, before plunging down to take prey in water; in still, calm conditions hovering used for 20% of dives, increasing to 80% in windy conditions. In Malawi, hovering was used for 98% of foraging on sandy beaches where perches rare, but for only 5% on rocky shores where perches common. Hovering allows it to go out over 3 km from shoreline; flies low over water then rises 2-10 m, with body nearly vertical, bill held down and wings beating rapidly; may move or drop down slightly and resume hovering before diving down; if successful, will swallow prey on the wing without prior beating on branch. Feeding success was 55% for dives from a perch and 41% from hovering on L. Victoria, but only 18% on L. Malawi with no differences between foraging methods. On L. Kariba, usual daytime feeding patterns with 4-5 peaks were moved to dawn and dusk to take advantage of sardine (*Limnothrissa miodon*) rising to surface; in Kashmir, was most active 08:00-09:00 and 16:00-18:00 hours. On land it will take termites on the wing, and will also dive to the ground to catch insects. Seen to hover over a clawless otter (*Aonyx capensis*), presumably watching for displaced fish. Sometimes uses hippopotamus (*Hippopotamus amphibius*) as a perch.

**Breeding.** Lays in Aug-Sept in Turkey, in Jun in Iraq, in Mar-Jun in Kashmir; mainly Feb-Apr in N India and mainly Nov-Apr in SE, in Mar-May in Sri Lanka, in Oct-Dec in Myanmar, in Dec-Mar in Thailand, and in Feb-May in SE China; in Mar-May in Egypt, in Sept-Apr in Senegambia, in Nov-Mar in Ghana and Nigeria, in Dec and May in Ethiopia; all months but mainly Mar-Jul in E. Africa; in Feb-Dec (mainly Jun) in Zambia, in Jun-Sept in Malawi, in Jul-Apr (mainly Sept-Oct) in Zimbabwe, in Apr-Oct in N Botswana and Namibia, and in Aug-Apr in South Africa. Breeds in pairs, or in family groups consisting of primary helpers (1-year-old son of one or both of nesting pair) and/or secondary helpers (unrelated males which not breeding), seldom more than 1 primary helper but can be several secondary in areas with poor food resources; primary helper involved at onset of breeding, bringing food to one of the pair, also helps to mob predators, joins in communal displays and helps to feed nestlings; secondary helpers initially driven off by male but more likely accepted soon after eggs hatch, particularly if food scarce. Solitary or in colonies of usually under 20 nests, but up to 100 reported in Zambia, colonial nests 0.5-5 m apart and defended by pair. Initial displays include aerial chases of 3-8 birds high over colony, then landing and displaying on open land with wing-spread posture and advertising calls, sometimes leading to a fight; male courtship-feeds female during nest-digging, laying and incubation; mating usually near nest, often follows courtship feeding. Nest in earthen bank, over water or up to 1 km from it, occasionally in flat grassy ground; excavated by pair and any primary helper by jabbing at soil with partially opened bill and then kicking soil backwards with legs; digging of tunnel usually takes c. 26 days (11 days to 11 weeks) and up to 80% of short holes without an egg chamber are dug; definitive nest-tunnel usually 1-2.5 m long, longer in sandy soil, straight, horizontal or slightly inclined, and ends in unlined chamber 45 cm long, 24 cm wide and 15 cm high; nestlings dig soil from walls for sanitation, so chamber becomes wider and lower with time. Clutch 1-7 eggs, usually 4-5, laid daily, starting c. 3 days after burrow complete; incubation period 18 days, starting with first egg, so hatching asynchronous over c. 3 days; female parent incubates and broods exclusively at night and also major part of day, assisted by male; young hatch blind and naked, initially fed mainly by male parent and any helpers, later also by female; nestlings fledge at 23-26 days, and 14 days later can fish for themselves, but stay with parents for several months. Breeding success 45-50%; in E. Africa, first-year mortality of males was 51%, and for adults average annual mortality was 45% in males and 54% in females. Sexually mature in first year, but some males do not breed until second year or later. Yearling females do not return to natal colony, and fewer adult females than males return to breed in same colony.

**Movements.** Generally sedentary. Many reports of seasonal changes in abundance, but these likely to be in response to changes in food availability rather than regular movements. Will arrive within a few days when dry rivers start flowing or when ephemeral pans fill. In non-breeding season, local movements can extend over several 100s of km. Also some observations of mass movements, but some of these may be of birds flying to large roosts of over 100 individuals. In Malawi, females tended to remain on nesting areas associated with rocky shores, while males tended to disperse farther, into areas with sandy shores. One bird ringed in Ethiopia was recovered in Uganda, 760 km away. A few records from Cyprus, Greece, SE Russia, Spain, Sicily and Poland.

**Status and Conservation.** Not globally threatened. Widespread, and one of the most numerous kingfishers in the world. Densities of 9-16 individuals/km were reported along the Kazinga Channel in Uganda, and 3-6/km on L. Malawi. On lakes of Uganda, Rwanda and elsewhere, densities of 2 birds/km of shoreline or less are more typical. Numbers have increased with the introduction of fish-stocking and fish-farming in several areas, and populations increased at Kampala, Uganda, by using sandpits for nesting. Has probably benefited from the construction of dams in many areas. Decreases in populations reported from parts of Syria, Israel and Egypt. In Botswana survived the spraying of endosulphan to control tsetse flies (*Glossina*), but elsewhere has been badly affected by the use of poisons to kill fish and Red-billed Queleas (*Quelea quelea*). Use of pesticides in sugar-growing areas of SE Zimbabwe may have led to widespread decline.

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Class AVES  
Order CORACIIFORMES  
Suborder ALCEDINES  
**Family TODIDAE (TODIES)**



- Small, rather plump kingfisher-like birds with long red bill, red gorget, and shining green dorsal plumage.
- 10-11.5 cm.



- Greater Antilles.
- Tropical forest and woodland, both primary and secondary.
- 1 genus, 5 species, 5 taxa.
- No species threatened; none extinct since 1600.

### Systematics

The five species of tody (*Todus*) comprise one of two avian families that are restricted solely to the West Indies, the other being the monospecific Palmchat (*Dulidae*) of Hispaniola. Todidae is an extremely uniform family. All species are morphologically and behaviourally similar, and as a group are so distinctive that their intrafamilial kinship has never been questioned, although early systematists had difficulty in determining the family's taxonomic position in relation to other bird families. Even as late as 1872, all tody species were normally regarded as "variations" of the Jamaican Tody (*Todus todus*), then often referred to as *Todus viridis*.

The genus *Todus* was established in 1760, when it was split from the kingfisher genus *Alcedo*. Thereafter, the todies were at various times placed within a remarkable assortment of putative "relatives": nightjars (*Caprimulgidae*), trogons (*Trogonidae*), jacamars (*Galbulidae*), puffbirds (*Bucconidae*), barbets (*Capitonidae*), kingfishers (*Alcedinidae*), motmots (*Momotidae*), broadbills (*Eurylaimidae*), cotingas (*Cotingidae*), manakins (*Pipridae*), flowerpeckers (*Dicaeidae*), and tyrant-flycatchers (*Tyrannidae*). Their true affinities were so obscure to early systematists that in 1882 it was proposed that they be classified in their own order, Todiformes, although this suggestion was subsequently rejected. Nowadays, it is generally agreed that they belong in the Coraciiformes.

Genetic research points to a relatively recent origin for the species that now comprise the family, indicating that the genus *Todus* diversified six million to seven million years ago. This agrees with earlier speculation that todies, or their ancestors, were able to cross the water barriers between the islands of the Greater Antilles within relatively recent geological time, perhaps even before the lowered sea-levels of the Pleistocene one million to 10,000 years ago. Unfortunately, todid paleontological clues are scant: a single todid ancestral fossil, *Palaeotodus emryi*, is known from the Oligocene of Wyoming, 37-24 million years ago, and a fossil todid has been described from the Phosphorites du Quercy, in France. The extinct *Palaeotodus* was larger than *Todus*, which is about 10.5-11.5 cm in length; its fragmentary remains suggest a size close to that of the 17-cm or so Tody Motmot (*Hylomanes momotula*) of Central America, but with a proportionately shorter and thicker bill. Its longer wings indicate greater powers of flight. Ossification of the cranial interorbital septum and the structure of the humerus link *Palaeotodus* and *Todus* most closely with the motmots.

In fact, the Tody Motmot, the most primitive momotid, may be the closest living relative of the todies. It is a little-known, solitary bird of the undergrowth in humid tropical and subtropical forest, where it feeds by sitting motionless for long periods, then darting out rapidly to capture prey in a manner similar to that of puffbirds and some other motmots. In its small size, short tail, pterylosis, and physical appearance, it resembles adult todies and the nestlings of larger motmots.

Many observers have commented on the large-headed appearance of modern *Todus*, a fact attributed by S. L. Olson in 1976 to the small size of todies having a secondary derivation. Todies are the smallest members of the order Coraciiformes; during their evolution they have displayed a common pattern, where body size changes faster than head size. Thus, small *Todus* species, derived from a larger *Palaeotodus*, would be expected to have a proportionately larger head.

Evidently, the common ancestors of both the motmots and the todies were originally widespread in the Northern Hemisphere. This is not surprising, since the Todidae and the Momotidae are the only truly New World families in the Coraciiformes; all the others originated in, and still occur in, the Old World. Osteological studies of *Palaeotodus*, along with similar examination of fossil and modern Coraciiformes, demonstrate that the todies probably evolved from a motmot-like ancestor in Europe. Bones from the extinct *Protornis glarniensis* of the lower Oligocene in Switzerland, a small motmot that was slightly smaller than *Hylomanes* and slightly bigger than *Todus*, provide evidence linking the motmots to the todies.

Several other characters link the todies more closely with the motmots than with the kingfishers. These include the serrated bill, with serrations which are microscopic in adults but motmot-like in nestlings; the presence of rictal bristles; a hook on the upper mandible, present only in the first few days in the todies and throughout life in the motmots; loose-webbed plumage; feather aftershafts; long pin-feathers; the huddling behaviour of chicks; and bone and musculature details. It should be noted here that the morphology and behaviour of immature birds have provided missing clues vital to the clarification of evolutionary relationships.

Combining geographical, paleontological, behavioural, morphological and genetic information, we can construct a fairly likely evolutionary scenario for the Todidae. More than 30 million years ago, "*Prototodus*", a hypothetical primitive, short-billed, motmot/tody-like ancestor resembling *Palaeotodus* or *Protornis*, is assumed to have existed in the Northern Hemisphere. At that time,



Now confined to the Greater Antilles, the modern-day todies are derived from an ancestor that is thought to have colonized the West Indies several million years ago.

The original colonizer of the archipelago would probably have arrived in Cuba from the Yucatán Peninsula, and thence spread to Hispaniola, Jamaica and finally Puerto Rico, evolving into five species in the process.

With its bright green upperparts, yellow lores and supercilia, blue carpal area and broadly pink flanks, the Cuban Tody is the most brightly coloured member of the family, and it is thought to be the oldest of the extant tody species.

[*Todus multicolor*,  
Zapata Swamp,  
Bermeja, Cuba.

Photo: Doug Wechsler/  
VIREO]



coraciiforms were common and widespread; indeed, during the Oligocene, they were at the height of their radiation. Between 20 million and 10 million years ago, as northern temperate climates cooled considerably, ancestral todies, now resembling *Palaeotodus*, disappeared from Europe while their distribution declined drastically in North America. By seven or six million years ago, reduced, relict populations evolved into *Todus*.

If *Todus* is at least six or seven million years old, and if, as recent genetic studies indicate, the northern and southern populations of the Narrow-billed Tody (*Todus angustirostris*) may have been evolutionarily independent for two million years, then the *Palaeotodus*-like tody ancestor, with its long wings, must have colonized the West Indies long before the Pleistocene glaciations of less than one million years ago, when lowered sea-levels greatly reduced distances between Central America and the Caribbean islands. The stage was set: the Greater Antilles were colonized from the west, speciation then occurring within the archipelago. Thus, the todies have probably been evolving in the Caribbean for several million years, rather than for less than one million as previously speculated.

Various lines of evidence, including morphology, particularly that of the plumage and the skeleton, as well as behaviour, vocalizations and ecology, suggest two natural tody groups which reflect their evolutionary history. The first of these comprises the Cuban Tody (*Todus multicolor*), the Broad-billed Tody (*Todus subulatus*) and the Narrow-billed Tody, and the second the Jamaican Tody and the Puerto Rican Tody (*Todus mexicanus*). Species in the first group all share bright pink flanks and perform striking "Flank Displays" utilizing the rosy tufts (see Breeding), whereas those in the second possess few or no pink flank feathers and such displays are absent or of very low intensity. Vocalizations are more complex, but the Cuban and, to a lesser degree, the Broad-billed are the only species that vocalize clearly, rather than uttering calls with a buzzy, nasal quality. The sounds uttered by the two species in the second group are almost identical to each other in their quality and duration. It should be noted, however, that very preliminary genetic studies recently carried out do not wholly support these two groupings.

In the West Indies, both avian evolutionary pathways and migratory routes are from west to east, against the prevailing winds. It is most likely that *Todus* first colonized the Greater Antilles from Yucatán to Cuba. The resultant Cuban Tody, the first newly evolved species, subsequently expanded its range to Hispaniola and Jamaica. Geographically, the Yucatán-Cuba pathway is more likely than the Nicaragua-Jamaica route, since it was the shortest route from Central America to the West Indies, even at the lowest Pleistocene sea-levels. Furthermore, the Cuban Tody was most probably the ancestral West Indian tody, since it is the most colourful, exhibits exaggerated displays, and has the widest ecological tolerance. It resembles "*Prototodus*" in its wing length and flying abilities.

In Hispaniola, the Cuban Tody apparently evolved into an ancestral Broad-billed Tody, as evidenced by the degree of pink, blue and iridescent green in the latter's plumage and the white mandibular "beard", together with its Flank Display intensity, vocalizations, posture and behaviour. Since Hispaniola's Broad-billed and Narrow-billed Todies are today the most specialized in terms of behaviour and morphology, presumably as a result of their sympatric distribution, it is difficult to tell whether they evolved when Hispaniola was divided into two islands in the Pleistocene by the higher sea-level or whether multiple invasions occurred.

In this respect, recent tentative work on the phylogenetic relationships of the todies based on mitochondrial DNA sequences may help to fill some gaps. The initial findings indicate a close affinity between the Narrow-billed and Puerto Rican Todies, suggesting colonization, possibly multiple, from Hispaniola to Puerto Rico, perhaps in addition to an original eastward path from Jamaica to Puerto Rico (see below). Moreover, Narrow-billed Tody populations in the northern mountain ranges of Hispaniola appear to be so genetically divergent from those in the southern ranges that the two may even represent distinct species.

Aspects of morphology and behaviour indicate that the Cuban Tody, after having reached Jamaica, evolved into a Jamaican endemic. The most obvious morphological link is the presence of blue-grey auriculars in the Jamaican Tody, which would ap-

pear to have derived from the sky-blue cheek patch of the Cuban Tody, a feature represented in other todids by only a few pale grey feathers. The two species are virtually identical in bill width and body length, and the intensity of wing-flicking is also the same, being less developed than in the two Hispaniolan species and more so than in the Puerto Rican Tody.

Continuing on through the Greater Antilles, the Jamaican Tody very likely colonized Puerto Rico. Although not predictable geographically, this movement across a relatively large stretch of water, bypassing Hispaniola, parallels the situation of the sibling Arrow-headed (*Dendroica pharetra*) and Elf-woods Warblers (*Dendroica angelae*), respectively of Jamaica and Puerto Rico. Alternatively, todies from Jamaica could have colonized Hispaniola en route to Puerto Rico, and then become extinct there. As alluded to above, their morphology and behaviour indicate that the Jamaican and Puerto Rican Todies are more closely related than are any other todid species pair. For example, the yellow-green undertail-coverts of the former evolved into yellow flanks in the Puerto Rican Tody. Both species exhibit low-intensity Flank Display because they possess few or no pink flank feathers. The greenish wash on the breast of the adult Jamaican Tody shows up in the juvenile Puerto Rican, while its blue-grey cheek patches have become reduced to a few pale grey feathers in the Puerto Rican Tody. Both species have identical bill widths and near-identical bill lengths, and both feed aerially to a greater extent than do other todid species. In addition, their vocalizations, especially the "Loud Beep" and contact notes (see Voice), are almost indistinguishable, and are far more alike in nasal quality and duration than are the vocalizations of the remaining species. "Throat-rattling", well developed in the Jamaican Tody, has its nearest counterpart in the seldom heard "Guttural Feeding Call" of the Puerto Rican Tody (see Voice).

## Morphological Aspects

Todies are tiny, round-bodied, large-headed, short-tailed birds which characteristically perch with the bill uptilted. Shining emerald-green above, and creamy below, with a prominent crimson bib, and a long, flat, bicoloured bill with the upper mandible black and the lower red, each bird resembles a miniature kingfisher. Their similarity to kingfishers and hummingbirds (Trochilidae) is enhanced by the tiny, plump body, crimson gorget, semi-iridescent plumage, occasional hovering behaviour, and convoluted, zooming displays. Indeed, todies resemble small forest-dwelling kingfishers to such an extent that Linnaeus mistakenly applied ■ kingfisher genus, *Alcedo*, to the first tody described, the Jamaican Tody. In Hispaniola, on the other hand, the local people refer to todies as *colibri*, a hummingbird name. The individual species of the Todidae are distinguished by differences in the colour of the flanks and belly, which can be pink and yellow or all yellow, by the presence or absence of small blue subauricular patches, a blue carpal patch and yellow-green supercilia, and by their vocalizations.

A "trademark" of the family, the scarlet gorget or bib, which is flecked with white in the Cuban and Broad-billed Todies, provoked interest and curiosity from even the earliest naturalists. For the first week, the fledgling's throat is pale grey and the blackish bill is about half the length of the adult's. The scarlet bib and a full-length bill take at least three weeks to develop, during which time the young birds are perfecting their feeding and flight behaviour.

The todid bill is flat, narrow and shallow, and is specialized for the family's principal feeding method, which involves snapping up insects from the undersides of leaves in short, sweeping forays (see Food and Feeding). The sideways movements used require the bill to be shallow, so that it can rapidly scoop up insects in the microspace between the insect's body and the undersurface of the leaf. The Cuban Tody has the smallest bill and the Broad-billed the largest. For the former, the culmen length, measured from the distal edge of the nostril, ranges from 12.3 mm to 14.3 mm, the width at the nostril is 3.9-5.4 mm, and the depth is 2.1-3.7 mm.

Like most tropical-forest birds, adult todies show no obvious differences in plumage through the course of the year. Nevertheless, the dull attire of an end-of-breeding adult, frazzled from raising three or four ravenous nestlings, can hardly be compared with the shiny, iridescent, breeding plumage, complete with dazzling, prominently displayed flank puffs (see Breeding). Tody feathers are rounded in shape, and loosely structured, this perhaps being related to the lack of need for streamlining, as the birds have a rather sedentary lifestyle and make only short flights, and to their characteristic fluffing displays.

Within the family, moult has apparently been studied only in the Jamaican Tody. It begins after breeding, with moult of the primaries starting in early August and that of the secondaries and rectrices from early September, with all flight-feathers replaced by the end of October. The primary feathers are shed descendantly, from the innermost outwards to the wingtip, and two or three can grow in simultaneously, as do the secondaries. The onset of secondary moult occurs at more or less the time when the fifth primary is fully grown. The secondary feathers are shed both ascendantly and descendantly, with the two waves of moult converging at S4 and S5. The rectrices are moulted centrifugally from the tail centre, beginning roughly when S1 and S8 are shed; the tail feathers are lost and renewed again quickly, so that they attain their full length almost simultaneously with the wing feathers. The body feathers are moulted at the same time, but the process continues for two months longer than that of the flight-feathers.

Although the todies are basically sexually monomorphic, within the genus there is sometimes a correlation between sex and iris colour. This is most obvious in the Puerto Rican Tody, where the male's iris is slate-coloured and the female's white, but the iris colour of the adult Jamaican Tody seems to be randomly white or slate. Interestingly, in the two Hispaniolan species, eye colour and sex are unrelated, but the eye colours of the species differ, being slate in the Broad-billed Tody and white in the Narrow-billed Tody. This specific difference perhaps serves as a reproductive isolating mechanism, additional such mechanisms in these sympatric species being micro-habitat and behavioural differences (see Food and Feeding). In the nineteenth century, naturalists thought that the iris of the male Cuban Tody was white and that of the female slate-coloured. Recent ringing studies indicate, however, that adults generally have white irides and that all juveniles have brown to grey or grey-blue ones; thus, eye colour may be age-related rather than sex-related.

The todies' short, rounded wings are in accord with their short flightpaths, small territories, feeding techniques (see Food and Feeding) and sedentary lifestyles. Within the genus, small differences in wing length correlate with differing flight distances. Data from nearly 5000 flight observations indicate that this correlation is most evident in the longest-winged species, the Broad-billed Tody. That species, with a mean wing chord of 50.3 mm, has the longest average flight distances, of 2.2 m, as well as the maximum flight distance recorded for the family, of 40 m. This is because it tends to occupy more open habitats, and within closed forest it forages higher in the trees. All other species have shorter wings, measuring 42.8-46.0 mm, and also exhibit shorter average and maximum flight distances of, respectively, 0.8-1.5 m and 7-26 m. They also do not forage so high up as the Broad-billed, and generally occupy more closed forest. Surprisingly, the Narrow-billed Tody, with both average and maximum flight distances the shortest of all the species, at 0.8 m and 7 m, and inhabiting the tangliest undergrowth, does not possess the shortest wings. At 46 mm, its wings are the second longest within the family, and this may be a result of its possible recent evolution from the longer-winged Broad-billed Tody (see Systematics).

When moving along perches, todies either flap once or twice, barely lifting the body, and hop sideways, or sidle like parrots (Psittacidae). Their tiny feet are warbler-like, appropriate for utilizing small-diameter twigs and branches. Average perch diameters range from 5 mm for the most diminutive species, the Puerto Rican Tody, to 11 mm for the largest, the Broad-billed Tody. Todies rarely visit the ground, and, when they do, hopping is their preferred gait, as it is with other coraciiforms.



The Narrow-billed and Broad-billed Todies are partially sympatric in Hispaniola, the only island inhabited by more than one species of today.

These two species are very similar in appearance, the main differences being that the former has a narrower bill, a black-tipped lower mandible, a whitish belly, and a pale iris, while the latter has a thicker bill, a solid red lower mandible, a yellowish belly, and a slate-coloured iris. The Narrow-billed inhabits wet montane forest at elevations of 1000-3200 m, whereas the Broad-billed frequents drier lowland scrub-forest and subdesert up to 1800 m; the two species overlap at the upper range of altitudes used by the Broad-billed Tody.

Differences in habitat use are reflected in the flight behaviour of the two species. Mean and maximum flight distances of the Narrow-billed are only 0.8 m and 7 m, in accordance with the dense forest they inhabit. In contrast, the corresponding values are 2.2 m and 40 m for the Broad-billed, which favours relatively open habitat. Where the two species overlap, the smaller Narrow-billed shifts its foraging height downwards, from a mean of 2.7 m in the absence of the Broad-billed to 2.3 m in its presence, and it tends to take smaller prey items. Mean foraging height of the Broad-billed is 3.1 m where the Narrow-billed is absent and 5.2 m where the two overlap.

[Above:

*Todus angustirostris*.

Below: *Todus subulatus*.



Sierra de Bahoruco

National Park,

Dominican Republic.

Photos: Doug Wechsler/  
VIREO]

## Habitat

Within their exclusively Greater Antillean range, all todies occupy diverse habitats, ranging in elevation from about 50 m below sea-level to over 3000 m above it. They favour brush and forest with interlacing or entangled twigs, leaves, epiphytes and vines. Todies generally fly only 1–2 m at a time, so they are rare in woodland where trees and bushes are spaced more than 3 m or so apart without intervening shrubby ground cover. Specific habitats include dry, mesic and wet forest on limestone karst; shaded coffee plantations; montane rainforest, including ridgetops and elfin woodland; dry lower montane forest; pine (*Pinus occidentalis*, *P. caribaea*) forest; second growth, including riparian woodland and pasture borders; subdesert with microphyllous shrubs, leguminous trees and *Cephalocereus* cacti; mangroves; and, in Cuba, littoral forest. Recent ringing studies in Cuba, where the habitats and micro-habitats used by migrant and resident birds were investigated in detail, appear to confirm that the tody shows no strong affiliation with any of the principal forest types. Indigenous palm stands, supporting low insect densities, are inhabited only rarely by the Todidae. Although these little avian jewels may centre their territories near forested residences, they are not “garden birds”. Nevertheless, the Jamaican Tody was found to occur at highest densities in areas with small woodland patches and intervening open pastures, and seemed to avoid pine forest. Moreover, it will even enter houses in pursuit of insects (see Relationship with Man).

The Narrow-billed Tody is the only species with restricted habitat preferences. The rarest member of the family, it prefers pine forest or dripping, high-elevation rainforest, where dense vegetation is festooned with climbing bamboo-grass, ferns, epiphytic mosses, leafy liverworts and orchids. The Broad-billed Tody, on the other hand, is virtually ubiquitous in Hispaniola in every lowland and mountain habitat, whether wet, mesic or dry. These two Hispaniolan species are particularly interesting because their ranges overlap; all other todies are confined to their own islands, where each is the sole representative of the family. In the Sierra de Bahoruco, the Broad-billed and Narrow-billed Todies occur together over a vertical range of at least 1200 m, resulting in marked differences between the two in micro-habitats and foraging behaviour (see Food and Feeding).

Three major factors limit tody distribution. These are minimum vegetation cover, relative insect abundance, and home-range or territory requirements, including the availability of banks suitable for nesting. There is considerable variation in population density depending on habitat quality and elevation. In general, territory size decreases markedly with increasing altitude. Pairs in smaller, contiguous territories defend them more often, and more vigorously, than do those occupying larger ones. On every island, the highest tody densities are found in shaded coffee plantations and in dry lowland or lower montane forest. In Luquillo, a prime Puerto Rican rainforest at an elevation of 130–1165 m, the tody's territory size averages 0.7 ha.

## General Habits

One's first glimpses and memories of todies are invariably of tiny, vivid green, rapidly bobbing birds uttering loud nasal “beeps” quite disproportionate to their size. The todies' short, rapid darts to snap insects from the undersides of leaves, as well as their aerial sallies from a stationary position, recall the behaviour of tyrannid flycatchers, especially that of the tody-flycatchers (*Todirostrum*). The loud “Wing-rattling” and “Wing-cracking” performed by todies during territorial and courtship chases (see Breeding) is reminiscent of similar behaviour shown by the manakins. It is understandable, therefore, that the todies were formerly thought to be related to both those families (see Systematics).

Although strictly territorial, todies may temporarily join mixed-species feeding flocks passing through their territories. This behaviour is most evident in autumn and spring, when Nearctic migrant warblers (Parulidae) are numerous and non-breeding todies are loosely paired. It is a common conception that all Neotropical feeding flocks are large, with high species

diversity, but this is not true in the West Indies, where the avifauna is impoverished compared with that of continental Central and South America. Caribbean feeding flocks are small, and irregular in occurrence. For example, in Puerto Rican rainforest, small flocks containing todies averaged only six species, united by the noisy, gregarious Puerto Rican Tanager (*Nesospingus speculiferus*); Bananaquits (*Coereba flaveola*), migrant parulid warblers, and a smattering of other residents, including thrushes (*Turdus*), vireos (*Vireo*) and other tanagers, comprised the remainder. In Hispaniola, which has a higher species diversity, eleven species were regularly present, centred around the Black-crowned Palm-tanager (*Phaenicophilus palmarum*). Interestingly, Broad-billed and Narrow-billed Todies, in addition to modifying their behaviour in areas where they are sympatric, also change their foraging tactics within mixed-species flocks.

All small, warm-blooded vertebrates face high energy expenditures. This is because of their high metabolic rates, exposure to lower temperatures at night, rapid heat transfer owing to their having a large surface area in relation to volume, and a limited capacity for amassing energy reserves through fat storage. For birds inhabiting rainforest, the need for energy and heat conservation is particularly acute, as foraging time is restricted during heavy rain, with the attendant risk of plumage-wetting, especially at high altitudes. Since todies are among the smallest and the most active feeders of all birds, it is only natural that they would have evolved effective modes of conserving energy. Surprisingly, they do not employ the typical coraciiform strategies of nocturnal thermoregulation, which involve roosting, often in groups, in nesting cavities, or in trees, huddling against one another. Instead, the todies rely more on physiological adaptations: low basic metabolic temperatures, controlled heterothermy, and torpor.

The Puerto Rican Tody exhibits a very low normal temperature of 36.7°C, rather than the 40°C more typical for other Coraciiformes. This enables it to decrease its expected energy expenditure by 33%, thus reducing the body's demand for increased metabolic heat production.

Most birds are homoiotherms. In other words, they maintain a basic body temperature, with little variation. A rare avian alternative to homoiothermy is heterothermy, a thermoregulatory pattern in which the bird's basic temperature is extremely variable. The Puerto Rican Tody utilizes this strategy. It is thus one of only a few tropical species, along with sunbirds (Nectariniidae), hummingbirds and manakins, that vary their body temperature according to that of their surroundings. Its surprisingly wide range of temperatures, 28–43°C, is actually a controlled response to environmental conditions. At low ambient temperatures, todies can decrease their basal temperature by up to 11°C. Their basal metabolic rates also vary geographically, representing an evolutionary adaptation to climatic conditions. Populations in semi-arid scrub-forest exhibit significantly lower temperatures than do those in cooler montane rainforest, perhaps because of the higher ambient temperatures in the semi-arid scrub and the todies' consequent need to prevent overheating.

True torpor is relatively rare among birds, having been recorded in only five other orders: swifts and hummingbirds (Apodiformes), nightjars and allies (Caprimulgiformes), mousebirds (Coliiformes), petrels (Procellariiformes), and one family in the Passeriformes, the swallows (Hirundinidae). The Puerto Rican Tody was the first of the Coraciiformes known to enter torpor, and the first of any avian species reported to exhibit sex-dependent torpor. Under experimental conditions, this controlled torpor saves todies around 70% of energy expenditure. A breeding-season phenomenon, it occurs only when hormone stress levels and metabolic rates are significantly higher than at other times. The increased energy demands associated with breeding may explain why torpor is apparently restricted to females. Although both sexes share in nest-building and parental care, the female must pay the additional energetic and physiological costs of egg-laying. This is particularly stressful for todies, since each egg, in a clutch of up to four eggs, weighs about 26% of the female's body mass. Although no corresponding data are available for birds, studies on Siberian hamsters (*Cricetulus*) indicate that high levels of testosterone in males inhibit torpor. Despite



The Puerto Rican Tody is by far the best-known member of the Todidae.

It is the smallest and drabdest tody and has the simplest displays.

It occurs in a wide variety of habitats, from arid lowland scrub to montane rainforest, and is rather common, though it can be difficult to find when it is perched beneath the forest canopy.

This individual exhibits the typical profile of a foraging tody, with its bill pointed upwards, as the bird rapidly scans the undersides of leaves for insects and other small invertebrates. Food is obtained by a short, upward dash known as an "Underleaf-sally".

[*Todus mexicanus*,  
Guánica Forest,  
Puerto Rico.

Photo: A. Greensmith/  
Ardea]



energetic stresses, a similar phenomenon in male todies during the breeding season might prevent them from entering torpor, although this is pure speculation.

Todies appear to delight in bathing, for which they employ one of two methods. In one of these, they touch the water surface with the body and wings as they skim above it, and then fly to a perch to arrange and preen their plumage. The other method involves exposing themselves to rain and the effects of wet foliage.

## Voice

Todies are constantly vocal, uttering simple, buzzy notes. Curiously, these unmusical calls, accompanied by peculiar bobbing postures, constitute some of these birds' most endearing qualities. The species differing most from this general pattern is the Cuban Tody, with its clear, lively, four-part, almost musical whistle. The other species have a marked nasal quality to their voices. Taken as a whole, sonagrams of tody calls, which all cover the same range of frequencies, rank among the simplest renderings of all avian vocalizations.

Adults also emit guttural sounds, known as "Throat-rattling", "Trilling", "Chattering", and "Soft muttering". Before fledging, juveniles utter high-pitched squeaks that develop into loud purring trills, these being especially loud when they are clamouring to be fed. Cloudy and rainy days suppress both activity and vocalizations, rendering todies much less conspicuous. Jamaican Todies are described as being rather silent outside the breeding season.

The Puerto Rican Tody, the most amply studied member of the family, utters six distinct sounds. It is most vocal from February to May, when its full repertoire may be heard. Its primary contact calls, the "Beep" and the "Loud Beep", resemble the call notes of parulid warblers, but are harsher, more emphatic and more buzzing. They can be heard throughout the year. The unmistakable "beep" sounds are single, short, nasal notes audible at distances of up to 50 m. Once heard, they are not easily forgotten. Activities such as foraging, chasing, entering a burrow, contacting an incubating partner in readiness for change-over,

or responding to a disturbance all elicit "beep" calls of varying sharpness, intensity and frequency. For anybody searching for todies, patient stalking in the general direction of these sounds will soon bring one into view. The "Bee-beep", "Beep-trill", "Muttering", and "Guttural Feeding Call" are virtually confined to the breeding season. All are accompanied by visual displays, which are described in detail later (see Breeding).

A discussion of todid vocalizations would not be complete without reference to "Wing-rattling", a loud whirring sound similar to the noise heard when pulling one's finger quickly across a comb, or that produced in the rapid whizzing pursuit of rival hummingbirds. It was first described in 1943, by T. Barbour, for the Cuban Tody: "The todies are tiny verdigris busybodies, far smaller than an English Sparrow [*Passer domesticus*]... and as they make each foray their wings snap like those of a giant grasshopper at each takeoff."

Dominant in the acoustic repertoire of all todies, this controllable, loud whirr is caused by air passing rapidly through the primary feathers. These primaries were once thought to be attenuated, but on close examination they do not appear to have any particular specialization such as shortness, stiffness or variable narrowness. Wing-rattling is easily confused with throat-rattling, and these two sounds may partly compensate for the family's poor vocal repertoire. Heard most often during the breeding season, Wing-rattling assumes its greatest importance during territorial and reproductive displays, varying in intensity from a feline purr to a manakin-like whip-crack. Despite its loudness, the sound carries poorly and is difficult to record. In rainforest it is greatly affected by weather: peaks of Wing-rattling follow peaks of sunny weather, and on any given day this characteristically todid whirr is likely to be heard during sunny periods, rather than in overcast or rainy spells.

## Food and Feeding

Todies prefer to forage in the forest understorey and require a plentiful, year-round food supply. They are largely insectivorous, and around 50 insect families have been identified as prey. These

are primarily grasshoppers and crickets (Orthoptera), beetles (Coleoptera), bugs (Hemiptera and Homoptera), moths and butterflies (Lepidoptera), flies (Diptera), cockroaches and mantises (Dictyoptera), lacewings and allies (Neuroptera), and bees, wasps and ants (Hymenoptera). Various other invertebrates consumed by todies include spiders, nematodes and millipedes, while insect eggs are also taken. The diet also includes vertebrates in the form of small anole lizards, and fruits from plant families such as the Brunelliaceae, Chenopodiaceae, Guttiferae, Moraceae, Papaveraceae, Rosaceae and Rubiaceae. In one study, small arthropods comprised 98% of stomach contents, with the remaining 2% being vegetable matter. The nestlings are fed largely on insects, and at an extremely high rate, but other foods are also occasionally brought to the nest (see Breeding).

The feeding behaviour of the Todidae has diverged considerably from that of its nearest relatives, the kingfishers and the motmots. The todies have carved out a niche that barely overlaps those of other Greater Antillean vertebrates. Their closest ecological counterparts on the American continent are the tody-flycatchers and the tody-tyrants (*Hemitriccus*). Considerably less active than warblers, todies typically fly less than 1.5 m per sally, and sit for several seconds before continuing to forage. The Narrow-billed Tody is the most active of the family, and the Broad-billed Tody the least active.

All members of the family capture insects by using a distinctive aerial feeding technique, known as the "Underleaf-sally". With bill and eyes directed upwards, the bird scans the undersides of leaves or twigs above its head. Alert, and jerking its head and eyes rapidly, it then darts upwards at a shallow angle and, in a short parabolic sally, snatches an insect and continues in an unbroken arc to another perch, rarely returning to the initial one. In xeric habitats, todies often swoop downwards to snap insects from the uppersides, rather than the undersides, of leaves, this being termed the "Sally-pounce". In addition to their characteristic mode of foraging from leaf undersides, todies also employ aerial and perch-based feeding manoeuvres. Occasionally, the bird will "Sally-hover" in mid-air, flycatcher-style, this being a common technique in open, dry habitats. Other feeding methods, including snapping, pouncing, sidling, reaching-up, jumping-up and probing, recall the foraging behaviour of various insectivorous families.

The principal foraging surfaces are leaves, fern fronds, trunks, branches, twigs, inflorescences, fruits, seedpods, and small vertical banks. Only rarely is food taken from the ground. Although not typically streamside-dwellers, todies occupy gulleys in lower montane areas, where they occasionally capture aquatic insects such as emerging adult mayflies (Ephemeroptera) and damselflies (Zygoptera). They will utilize any perch sturdy enough to support them, with recorded perches ranging from 1 mm to 60 mm in diameter, and including twigs, vines, petioles, branches, palm stipes, ferns and flower peduncles. They prefer a 360° view, however restricted.

Todies feed primarily in the low to middle strata of the forest, often at the observer's eye level. The mean foraging height for all species is 2.3 m in xeric scrub and 4.9 m in rainforest. The fact that these birds can be easily seen, and can be approached to within a few metres, is probably one reason why they have endeared themselves to islanders. The Broad-billed Tody feeds much higher up than other species, this behaviour being accentuated in areas where it occurs alongside the Narrow-billed Tody. Thus, the two Hispaniolan species exhibit both micro-habitat differentiation and behavioural-character displacement when occurring sympatrically. This resource-partitioning is reflected not only in foraging heights, but also in flight lengths and angles, number of flights per minute, number of successful captures per minute, duration of perching between flights, and general feeding efficiency. The Broad-billed Tody occurs in xeric scrub and in coffee and pine plantations. Its average foraging height was found to be 3.1 m where the Narrow-billed Tody was absent, increasing to 5.2 m where the two species occurred together. This contrasts with a corresponding decrease in foraging height in the Narrow-billed Tody, from 2.7 m to 2.3 m. Where they co-exist, the Broad-billed Tody flies higher, into more open canopies, utilizing longer sallies than otherwise, and capturing larger prey,

while the Narrow-billed drops into the denser understorey, where shorter flights, near-perch jumps, and the taking of smaller prey are more advantageous.

Todies have voracious appetites. For example, in El Verde, a lower montane rainforest in Puerto Rico, it is estimated that one family consumed approximately 1.8 million insects on a 0.7-ha plot during 5.5 months, the average period over which todies vigorously defend breeding territories.

The Todidae were previously thought to exhibit uniquely fast metabolic rates. The evidence for this stemmed from a captive bird which consumed the equivalent of 40% of its body mass daily, and from a detailed three-year study that included 5200 feeding observations of all species. Over the year, feeding rates throughout 14-hour days averaged 1.9 per minute in xeric scrub and 1.1 per minute in rainforest. Recent physiological research, however, has determined that, although the metabolic rates of todies are very high, they compare favourably with those of other tiny birds such as the Magnificent Hummingbird (*Eugenes fulgens*) and the Goldcrest (*Regulus regulus*). The shortness of the tody intestine, barely 7 cm long and roughly equal to the bird's body length, is a good indication of how rapidly food passes through the alimentary tract.

## Breeding

So far as is known, todies are monogamous. Their courtship displays involve the male and female chasing each other closely, "Wing-rattling" and "Wing-cracking" vigorously. They pursue each other, often at lightning speed, on straight flightpaths or in parabolic arcs or circles, darting and weaving among low foliage, covering distances of up to 10 m. Most chases result in multiple body contacts, and may involve tumbles. When at its height, tody display resembles that of manakins, except that the todies usually pursue each other in and out of tangled vegetation, rather than in open arenas. Stationary displays are also agitated, the perched bird hopping and bobbing rapidly, with frequent plumage-fluffing.

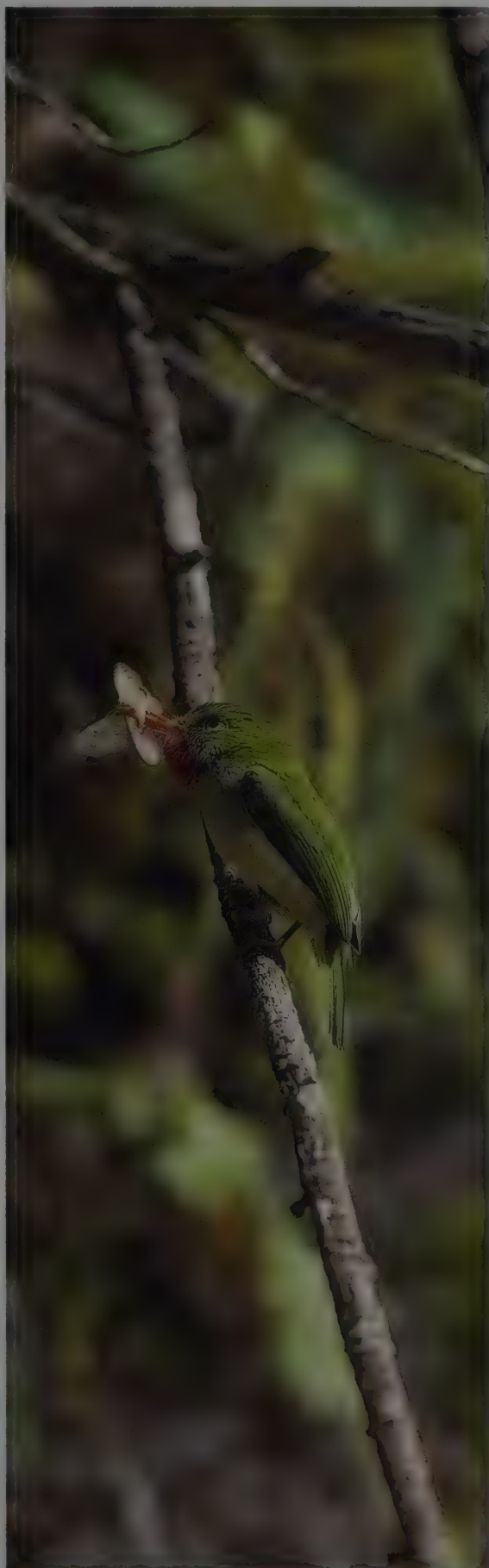
The second most important component of pre-copulatory behaviour, and a highly attractive one, is the "Flank Display", common to all species except the Puerto Rican Tody. It is most highly developed in the pink-flanked todies, namely, the Cuban, the Narrow-billed and the Broad-billed. In this display, the stunning rosy flank feathers are fluffed to varying degrees depending on display intensity. When this is at its height, the tody's tiny body is completely "inflated" into a circular fuzball of green down, with wings barely visible, and the bright rosy tufts almost meeting over the back. The degree to which the colourful flanks extend backwards, and the amplitude of dorsal wing-flicking, are directly proportional to the volume of pink feathers. The most striking displays are those performed by the Broad-billed Tody, followed by the Cuban, Narrow-billed and Jamaican Todies, bearing decreasing amounts of pink. The Puerto Rican Tody, entirely yellow-flanked, rarely fluffs out its plumage so completely as do the other species, and never flicks its wings above the back.

Courtship feeding occurs, but is not always an essential preliminary to mating. After chasing, one partner flies towards the other, landing or hovering for a moment while presenting the partner with an insect. This "present-exchange" may occur two or three times in succession before regular feeding is resumed. In addition to its role in courtship, mutual feeding strengthens the pair-bond during incubation and nestling care, or even immediately after a brood is lost to a predator. The female invites copulation by flapping her wings, then spreading them and raising her short tail.

Territory sizes vary, depending on habitat. Those of the Puerto Rican Tody average 0.7 ha per pair in lower montane rainforest, but at higher elevations, where stunted elfin forest supports lower insect densities, they are almost three times as large, averaging 2 ha. Territories are also larger in forested flats, in boulder-filled ravines, and in open stands of second growth where suitable nesting banks are limited.

Todies are burrow-nesters, as are most of the Coraciiformes. The first, and rather delightful, published description of the nest-





Todies feed on a tremendous variety of insects, especially flies, beetles, grasshoppers, crickets and moths, but they are also known to take spiders, nematodes, millipedes, small lizards and the occasional fruit.

They generally avoid preying on stinging wasps, bees and houseflies, even when these are locally abundant. Prey items are often rather small, although this Jamaican

Tody has captured a moderate-sized moth.

The foraging behaviour of todies is vastly different from that of their nearest relatives, the kingfishers

(Alcedinidae) and motmots (Momotidae).

Indeed, their principal method of scanning the

undersides of leaves, sallying up to snatch

a prey item, and then moving to another perch is

so specialized compared with the foraging

behaviour of other West Indian vertebrates that

todies have few direct competitors for food.

The diets of todies probably overlap

most with those of the migrant wood-warblers

(Parulidae) that winter in the Caribbean and

with some of the tyrant-flycatchers (Tyrannidae)

that are permanent residents in the Greater

Antilles, including several species of pewee

(Contopus) and the Puerto Rican Flycatcher

(Myiarchus antillarum).

[*Todus todus*, Jamaica.

Photo: Sean Morris/Oxford Scientific Films]

ing habits of a tody comes from a Mr Moritz in Puerto Rico, in 1836: "In shady trees is seen once in a while the lovely green San Pedrito, rattling hoarsely ... The locals believe that it nests in holes in the earth."

Amongst the most diminutive of all bank-nesters, todies also dig the shortest burrows. They excavate cylindrical, angled tunnels in vertical soil embankments. Banks commonly selected are amphitheatre-shaped slippages, trail or roadside cuttings, or natural inclines away from easily flooded rivers and ravines, and they are not high, usually less than 1.5 m. Although nest-tunnels may be gouged out of bare banks, the most successful are those in moderately overgrown, obstacle-free inclines, the plants providing soil stabilization and partial concealment from mongooses (*Herpestes*). Banks laden with abundant vegetation, on the other hand, are difficult to excavate, since the todies must sometimes tear away several centimetres of thick mosses and liverworts before reaching the wet, sticky soil. In Jamaica, todies sometimes remove stones from banks, thereby facilitating smooth entrances to their nesting-tunnels; at times, they will even transport stones as large as 2.5 cm by 1 cm for distances of up to 3 m in the bill. In xeric scrubland, chalky banks that are easily excavated are preferred. These are often simple knobby irregularities close to ground level. The tunnels made by todies are normally horizontal, and only rarely inclined. In one study, 86% had a curve of roughly 90°, an equal proportion of these being directed to the right as to the left. The tunnel terminates in an enlarged, depressed, unlined chamber, where the eggs are laid on the bare, compact earth. Burrow lengths of the different species range from 12 cm to 60 cm, with much intraspecific variation; hole diameters average 3.4-4.4 cm.

Unusual nest-sites recently found in Cuba have been within a cave, along with Cave Swallows (*Hirundo fulva*), and in crab burrows. The latter is the only known example of todid nests in a horizontal substrate, as opposed to a vertical bank. Todies will also, albeit rarely, excavate holes in dead wood, or adapt a hole started by a woodpecker. One pair of Jamaican Todies nested in a cleft in a stone wall.

Since todies retain their home ranges throughout the year, and defend the same breeding territories each year, they generally excavate in association with previous burrows. This is due partly to the fact that "tody banks" are not evenly or abundantly distributed within any habitat. The todies begin roughly three times as many tunnels as they actually use. The reasons for this are varied, and include the selecting of sites with unsuitable soil, the presence of obstacles such as roots or stones, or insufficient plant cover, bank slippages after heavy rains, poor burrowing techniques, rapidly growing ferns or roots which obscure the hole, and earliness of the season. They always abandon nests which become flooded.

Fresh tunnels are dug each year. The overall burrowing season lasts nine months, from September to June, but is concentrated from February to May. Todies inhabiting rainforest normally build nests and lay eggs during the driest part of the year, but during unusually long, island-wide dry seasons breeding activities may begin three or four weeks earlier. Conversely, todies inhabiting xeric scrub, with rainfall half that of the rainforest, breed as far as possible into the "wet" season; it should be noted, however, that in a Puerto Rican study area annual rainfall averaged 600 mm over three years, so that it was almost always very wet. Digging activity is irregular, with the result that each burrow requires about eight weeks for completion. In the early phases, trips to the hole during a stint of digging are numerous, with up to 60 visits per hour, and are accompanied by vigorous, even frenzied activity. The long, strong bill of the tody acts as a chisel, closely gouging out the soil during thrusting bouts, between which the bird returns to a favourite perch. After the initial stages, the birds scrape out fresh dirt with their tiny feet. Irregular bursts of hyperactivity settle into a flexible morning routine, characterized by digging for 15 minutes and then foraging for 45 minutes in each hour. Cloud and rain suppress digging, which ceases altogether in the afternoon. When soil in the chamber is compacted and the burrow is in use, the passage of the adults' feet leaves two unmistakable parallel grooves on the lower sides of the tunnel. During excavation, the pair-bond is very much in evidence.

Male and female excavate alternately, communicating with low, ventriloquistic muttering sounds. Both sexes vigorously defend their nesting territories from trespassers, be they other birds, people or mongooses.

Naturally, the neatly excavated burrows attract non-avian hole-nesters, which may take up residence at any time during the todies' breeding cycle. Unwelcome occupants ousting these industrious little birds include tree-frogs (*Eleutherodactylus*), lizards (*Anolis*), scorpions (*Tityrus*), stinging ants (*Solenopsis*), cave crickets (*Amphicausta*), and a "tarantula" (*Cyrtophilis*). Surely one of the most intimidating must be Puerto Rico's large whipscorpion (*Phrynos palmata*), a nocturnal predator with long, spidery appendages, common in the lower montane forest, which seeks dark mini-caves. Rather fearsome even to a human, it is longer than a tody. Its enormous, powerful, viciously spined pedipalps, normally used to squash other arthropods, are three times as long as a tody egg and twice as wide. Some todid tunnels are built in situations where they are exposed to the sun, and this could be a strategy against light-avoiding predators such as large spiders.

Tody eggs are ovate and glossy white, with a fragile shell, and are equivalent in size to those of the smallest wrens (*Troglodytes*) and slightly larger than those of most hummingbirds. In life, the eggs are tinged rosy owing to the large orange-red yolk, a reserve required for their relatively long incubation. Despite the tody's small body size, the egg weight of 1.4 g represents a remarkable 26% of the adult's body weight, an extremely high percentage for any bird, and akin to the eggs of kiwis (*Apterygidae*) and storm-petrels (*Hydrobatidae*). In most birds, the ratio of egg weight to adult body weight is within the range 1.8–11%.

One to four eggs are laid from March to July, with peak laying times differing according to habitat and weather conditions. Todies lay on consecutive nights until the clutch is complete. One clutch is laid annually, which is typical of the Coraciiformes, although, if the eggs are destroyed, todies may attempt to breed once or twice more. Only in extremely rare cases, however, do they raise more than one brood per year.

Both sexes develop brood patches, and both incubate. From the limited data available, the incubation period is probably 21–22 days. Todies appear to be inattentive parents, each adult spending less than one quarter of its daylight hours incubating. Motmots and kingfishers are far more assiduous, spending up to seven continuous hours on eggs, and keeping them almost constantly covered; the Ringed Kingfisher (*Megasceryle torquata*), for example, changes over only once a day. These short, irregular incubation intervals suggest that todies need to feed far more often than their larger coraciiform relatives, seemingly for more than three-quarters of their waking hours, in order to survive.

Todies do not show any elaborate greeting ceremonies at the nest, which is, again, typical of the Coraciiformes. Because immediate change-over is rare, the parents are generally silent when they enter and when they leave. When any signals are given, they consist of one or two short, sharp "beep" notes and a whirr of wings as the adult whizzes into the nest-hole.

Hatching occurs principally in the late afternoon, the process taking less than one hour from pipping, an extremely short time compared with most other birds. It is asynchronous, indicating that incubation starts with the first egg. One adult remains in the nest-chamber during hatching, and there is no evidence that shell fragments are ever removed.

The chicks are altricial, with no natal down and with conspicuous heel callosities. An adaptation to hole-nesting, these cushioned heels, covered with a thick pad of swollen skin and numerous tubercles, are present from hatching to fledging. In either smooth or nodulose form, they are present in many nestlings, especially those of the Coraciiformes, that are nurtured within unlined nests in earth burrows, tree holes or termitaria.

The nestling period of the Puerto Rican Tody, by far the best-studied member of the family, is 19–20 days, during which time the chicks seem to be brooded as inattentively as the eggs are incubated. The parents average only six minutes of brooding per visit during the first week, after which several days elapse before the nestlings have the homoiothermic benefit of their own down.

Partly to offset the lack of parental warmth, and to assist thermoregulation, young chicks huddle together, their wings and heads interlocked in a mass of fleshy pink balls; in cases where only a single chick is present in the nest, it is unclear what behaviour it adopts to counter any lack of warmth, and whether it suffers through chilling. When the first, loose feathers appear, they are dull green with grey, downy bases.

When it comes to feeding their chicks, however, todies are diligent parents, bringing their offspring enormous quantities of insects. From hatching onwards, it appears that foraging is more crucial to the survival of the young than is brooding. In many birds, adults reduce the volume of food fed to chicks as the latter near fledging, but this is not the case with the todies. In fact, the highest feeding rates recorded in one study were just prior to fledging, when 420 feeds per day were delivered for a brood of three, one of the fastest rates recorded for any species of insectivorous bird. Normally, single items of food are brought, and the nestlings do not waddle to the nest-hole entrance to receive these. The principal nestling diet is insects, primarily Homoptera, Coleoptera, Lepidoptera, Orthoptera and Hemiptera. One fascinating aspect is the marked selection in the size and variety of insects caught, corresponding to chick age. Adult todies discriminate in the type and size of food they bring to the nest. For example, in the initial stages they deliver tiny flies, beetles and bugs which are less than 3 mm long. At an early point, when the young themselves are 40–50 mm long, there is a sudden increase in the diversity of prey, and small grasshoppers, palmhoppers, cockroaches, moths, spiders and lanternflies up to 25 mm long are added to the diet. Soon, the chicks accept varieties of prey items that are up to 40 mm in length, such as caddisflies, lacewings, soldierflies, stick-insects, long-horned grasshoppers, stout caterpillars, and brightly coloured pupae. This extends into the post-fledging period. Interestingly, at one Puerto Rican Tody nest, 18% of 163 feedings over 7.5 hours were of the small fruits of the tree *Clusia krugiana* (Guttiferae). Unlike kingfishers and jacamars, todies do not regurgitate chitinous pellets in the chamber, and they even remove uneaten moth wings. No other form of nest sanitation is performed.

Nest-helping by one or two other adults during the incubation and nestling periods is common in the Puerto Rican Tody, although there are no data available to show whether it occurs also in the other members of the family. The todies exhibit many of the characteristics of other avian co-operative breeders, including insectivory, monogamy, a single annual clutch, and a tropical distribution. Preliminary information from two independent studies in Luquillo Forest indicated that at least 50% of breeding pairs of Puerto Rican Todies were assisted by unidentified helpers. Nests with additional helpers contained significantly larger clutches, with a mean of 2.9 eggs, than did those without, which averaged 2.3 eggs. In some cases, helpers assisted during the later stages of incubation, and the time spent incubating by each parent was then even less than the one-quarter of daylight hours mentioned above. Moreover, not only were chicks more advanced morphologically and behaviourally during the entire nestling period than were young in nests with fewer attendants, but broods fed by four adults fledged one to two days earlier than normal. Since helpers typically increase the amount of food brought to the young, more rapid nestling growth and a shorter nestling period are to be expected at nests favoured by helpers. Conversely, inattentiveness by the parent birds, owing to poor weather, for instance, may retard chick growth by two or more days.

Kin selection has been the focus of most attempts to explain co-operative breeding. In most cases, young of the year remain to help defend their natal territory during the non-breeding season, and they are related to the chicks which they later help to raise. This is evidently not the situation with Puerto Rican Todies, so that, in their case, kin selection is probably not the principal evolutionary force resulting in nest-helping. Support for this statement derives from several factors: all territories studied have contained only two adults; territorial birds at first repelled helpers; helpers do not assist with tunnel excavation, appearing only late in the incubation period and during the nestling period; subadults disappeared from the natal territory within three months;



This Jamaican Tody has captured a small caterpillar, a typical prey item for the species. Todies have seemingly insatiable appetites: one captive consumed nearly 40% of its body mass in insects per day, and capture rates in the wild can average up to 1.9 prey items per minute. A pair of Puerto Rican Todies (*Todus mexicanus*) and their two helpers delivered an estimated 280 prey items per day to a brood of two nestlings, and another breeding group of this same species brought 420 items per day to a brood of three, resulting in some of the highest feeding rates ever recorded for a bird.

[*Todus todus*,  
Jamaica.

Photo: Sean Morris/  
Oxford Scientific Films]



and known ringed nestlings never returned to the natal territory after post-fledging dispersal. It appears that, with Puerto Rican Todies, helpers are not young from the previous year that have deferred breeding, whereas they typically are among many co-operative breeders.

Thus, nest co-operation among Puerto Rican Todies is unlike that of any other bird species studied, because of the apparent absence of a genetic relationship between helpers and recipients. In other words, helping at the nest has developed in the absence of extended family groupings. Helpers are most likely adults from nearby territories the breeding activities of which have been curtailed, or which did not breed at all. Since todies rarely raise second broods, it seems natural for suppressed breeders or unpaired "floaters" to attach themselves to nearby nesting pairs, and in this way move among territories, as happens with the Brown-headed Nuthatch (*Sitta pusilla*) and the fairywrens (*Malurus*). An alternative possibility is intraspecific nest parasitism. One potential evolutionary reward for helping behaviour is shared parentage in a larger, co-operatively raised brood. Preliminary data on Puerto Rican Todies indicate that nests with helpers rear significantly bigger broods, but no genetic studies have been undertaken to determine whether the parentage of brood-members extends outside that of the two paired adults. Further fieldwork needs to be carried out on nest-helpers among the Todidae.

Two or three days prior to fledging, the adults hover at the nest-hole, uttering "beep" calls, bobbing, and acting in an agitated manner for hours on end. In response, the chicks emit loud trills. During the first five weeks, the fledglings rarely venture farther than 25 m from the nest, but they never return to it, even to sleep; initial observations indicate that, once fledged, they are led by their parents into a nearby tree to pass the night, huddling close together on tiny perches. The parents feed the fledglings for three weeks after emergence, mostly during the first week. They use several methods to encourage the young to become independent. These include pushing them off perches, hovering in front of them with food and then pulling it away at the last second, and landing a short distance from a chick and forcing it

to move to obtain its food. Sometimes the adult male intervenes, preventing the female from feeding the fledgling, a type of behaviour that appears only at this late stage of chick-rearing; up to this point, both adults have shown themselves to be the most assiduous of parents.

Because of the nature of the foraging styles employed by todies, the fledglings generally take longer to perfect them than do the young of many insectivores. The timing is much as that of the gnatcatchers (*Poliophtila*). At first, when the young todies are developing multidirectional feeding co-ordination, they judge distances poorly and cannot pre-plan precise landings, a trait typical of most young birds. Fledglings pass through four developmental stages, each of a different duration, until adult morphology is acquired after about 42 days. The definition of each stage is based on bill length, throat colour, degree of chick independence and flight proficiency, along with numerous other behavioural details. The entire repertoire of adult behaviour is not achieved for several months. Wing-rattling, for example, first appears at four months.

Not unsurprisingly, little is known of the longevity of the Todidae. Ringed Jamaican Todies have been recorded as surviving to an age of seven to eight years, and this may be fairly typical of the family as a whole, but no other data are available.

## Movements

Todies are non-social birds, living in pairs which establish individual breeding territories. They remain in these throughout the year, and retain them from one year to the next. During the non-breeding months, they forage in larger home ranges which include neighbouring territories. They never form intraspecific feeding flocks, but may temporarily join mixed-species flocks that pass through their territories (see Food and Feeding). From all the evidence available, therefore, the todies are essentially resident, showing no signs of any true migratory movements. This is a characteristic of the majority of bird species which breed in tropical-forest areas.

Until the 1990's, todies were considered to be entirely sedentary. Preliminary fieldwork in the Cordillera Central, in Hispaniola, indicates, however, that Narrow-billed Todies may undertake short, seasonal movements. This species appears to move during the cooler months down to lower elevations, returning to higher altitudes to breed.

Information on the post-breeding dispersal of juveniles from the parental territory is lacking. Nevertheless, it would seem likely that young todies do not move far, probably no more than a few kilometres at the most, to the nearest suitable territory that is available.

## Relationship with Man

Despite their tameness and abundance in a variety of West Indian habitats, todies were apparently never culturally important, apart from their role in providing a source of mini-snacks. Local people bestowed upon them a variety of endearing names. Their bank-nesting habits prompted the French *Perroquet de Terre*, meaning "Parakeet of the Earth", and the Spanish *Barrancoli*, *Barranquero* and *Barrancolino*, these last names derived from *barranco*, a Spanish word for "bank". The tiny size of these birds led to the colloquial name *Medio Peso*, or "half-dollar", in Puerto Rico, and an understandable confusion between the todies and the hummingbirds inspired the name *Colibri* in Hispaniola.

Onomatopoeic names such as *Pichui* and *Chicorette* reflect the vocalizations of the Todidae. A common vernacular name in Puerto Rico is *Papagayo*, a name otherwise applied to parakeets and suggesting loud noise. The Cuban Tody is often known as the *Pedorrera*, a rather malodorous term referring to the noise made when breaking wind; this name may relate to the Wing-rattling behaviour of the tody.

Bird-loving Englishmen in Jamaica chose to call the local tody the "Robin Redbreast", clearly an allusion to the bird's red bib, friendliness and abundance, which would have recalled to the settlers the European Robin (*Erithacus rubecula*) which they knew so well back in their homeland. The "Redbreast" commonly allows people to approach to within 2-3 m, at times to less than 50 cm, and indeed is not averse to entering houses in its pursuit of insects, even making use of such useful perches as curtain rails.

## Status and Conservation

As a family, the todies seem reasonably secure. Only the Narrow-billed Tody gives cause for concern, and is considered to be Near-threatened. Overall, however, the todies are still common to abundant in most natural and man-modified arboreal habitats of the West Indies. They have partly benefited from man's activities, building their burrows in road cuttings, roadside banks and drainage ditches; greater densities are found in these habitats than elsewhere. Sadly, they often dig burrows before sufficient plant cover has stabilized the soil, and many nests are unsuccessful owing to slippages or mongoose predation. Todies do not benefit from clear-cutting or urbanization, and they could never be thought of as birds of pastureland or gardens. Only once has a tody been reported utilizing a man-made object: a pair of Jamaican Todies nested in a wooden flowerpot, entering through a hole in the side and tunnelling into it to lay eggs. Decades ago, on the Isle of Pines (Isla de la Juventud), the Cuban Tody resided in grapefruit orchards. It is not known whether this is still the case today, although todies do not generally adapt to orchards and gardens.

It is clear that there is a positive correlation between insect abundance and tody populations. The highest insect densities are in warmer habitats at low altitude, those that are first altered by man. At higher elevations, where insect populations decrease, the home ranges of todies expand, their populations thin out, and they are more climate-dependent. Little information is available on the increasing use of pesticides, a potential complicating factor considering the todies' voracious appetites (see Food and Feeding). On Cuba's Cayo Coco, currently undergoing rapid tour-

ism expansion, Malathion is sprayed aerially on wetlands and forested areas, and hand-held "fogging" sprayers are commonly utilized around beachfront hotels. The potential consequences of the use of these insecticides are damaging for the highly insectivorous tody populations.

In the past, coffee was an important cash-crop in the Greater Antilles. *Cafetales* consisted of coffee bushes grown under tall, shady, indigenous trees. In recent years, coffee corporations have found that economic rewards are greater, though the quality of the product is poorer, if coffee is grown under direct sun. In the old-fashioned *cafetales*, todies enjoyed healthy populations and, in turn, controlled insect numbers. They are not adapting well to present-day commercial coffee plantations, in part because natural irregularities in the terrain, which provide nesting banks, are often smoothed out by bulldozers in order to create a more uniform, more easily harvested crop.

Another possibility to be considered is the effects of global warming on world climate, particularly if this leads to even higher rainfall in the Caribbean. During torrential rains, todies have trouble finding sufficient food for themselves and their nestlings, because insects hide away or are washed from leaves. In addition, nesting banks suffer slippage. Both these factors reduce breeding success.

Although natural predators are an inevitable part of the life of any bird, introduced predators are the greater menace. Todies are seriously affected by the predatory Indian mongoose (*Herpestes auropunctatus*), which accounted for 81% of nest failures in Puerto Rico's Luquillo rainforest. Since mongooses are rarer in xeric habitats, owing to a scarcity of fresh water, todies suffer fewer adverse effects there. Unfortunately, mongoose eradication would be a serious undertaking on such large islands, and a very difficult one in which to achieve any real success.

As the world's human population grows inexorably, predation by man may increase. Puerto Rico is sufficiently prosperous for todies not to be unduly bothered by children seeking supplementary protein. Elsewhere in rural areas, however, where people eke out subsistence-level lifestyles, children, as well as mongooses, dig out tody holes for eggs; the adult birds are also trapped, or killed with slingshots. Since the nest-holes of these birds are frequently concentrated along roads and trails, they are highly susceptible to this type of predation. For example, in a six-hour climb along a jeep track in Hispaniola, as many as 20 old tody burrows were found, all of which had dug out by humans.

It is to be hoped that todies will continue to be a distinctive and delightful feature of West Indian wooded habitats. This will happen only with the preservation of forest swathes in areas of irregular topography. Todies could be easily encouraged in any wooded habitat, especially coffee plantations, by the provision of man-made nesting banks in accordance with the sizes of their breeding territories, which are about 0.6-1.0 ha in wet forest. Captive-breeding of these tiny, specialized birds is extremely difficult, and is not a viable option.

As a tribute to the eminent ornithologist-adventurer A. Wetmore, also an admirable gentleman, his 1927 description of todies may serve as an inspiration for the future protection of Caribbean environments:

"If there be gnomes and elves in our world of birds, among them are the tiny todies, whose long, spadelike bills, light eyes, brilliant plumage and peculiar mannerisms make them the dwarfs and hobgoblins of the West Indian forests ... their acquaintance is one of the greatest pleasures that comes to a foreign ornithologist travelling in their haunts."

## General Bibliography

Bock (1994), Bond (1948), Brodtkorb (1971), Burton (1984), Clark (1913), Cracraft (1981), Forbes (1882), Forshaw & Cooper (1987), Kepler (1972, 1977, 1985), Lowe (1948), Maurer (1978), Maurer & Raikow (1981), Mourer-Chauviré (1985, 1988b), Murie (1872b), Nosedal (1981), Olson, S.L. (1976), Peters (1945), Ricklefs & Bermingham (1997), Schuchmann (1982), Sclater (1872), Sibley (1996), Sibley & Ahlquist (1972, 1990), Sibley & Monroe (1990), Sibley *et al.* (1988), Verheyen (1955a, 1955b, 1955c).



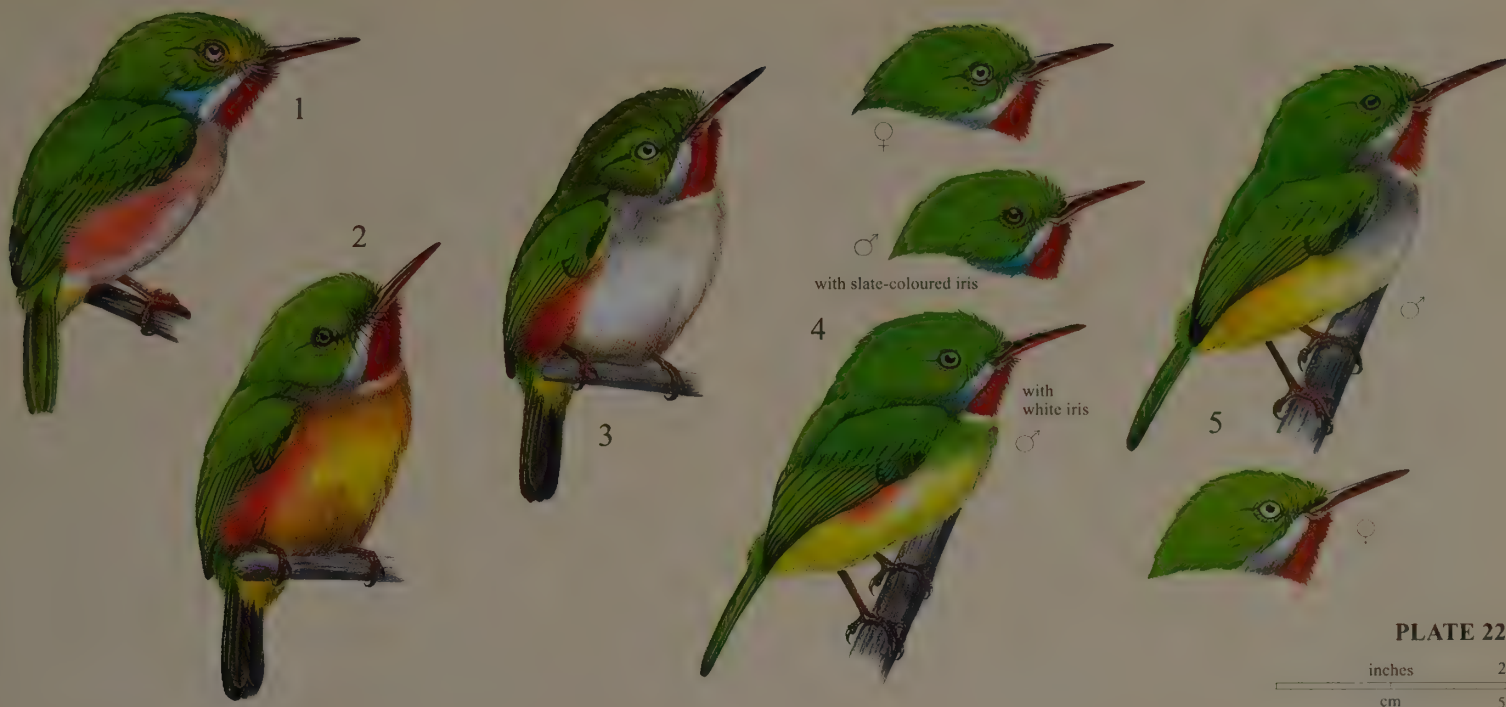


PLATE 22

## Family TODIDAE (TODIES) SPECIES ACCOUNTS

## PLATE 22

### Genus *TODUS* Brisson, 1760

#### 1. Cuban Tody *Todus multicolor*

**French:** Todier de Cuba **German:** Vielfarbenetodi **Spanish:** Barrancoli Cubano

**Taxonomy.** *Todus multicolor* Gould, 1837, no locality = western Cuba. Birds of E Cuba have been separated as race *exilis* on basis of slight colour differences, but these are generally considered insufficient to warrant subspecific recognition. Monotypic.  
**Distribution.** Cuba, including larger cays off N coast (Coco, Romano, Guajaba, Sabinal, Saetia), and I of Pines.



**Descriptive notes.** c. 10-11 cm; 5.2-6.7 g. Most brilliantly coloured tody, with smallest bill. Bright green above; yellow-green, almost iridescent supercilia, yellow lores; prominent sky-blue patch below ear-coverts (deeper blue on birds from I of Pines), also sky-blue carpal area; much pink on flanks; whitish belly, yellow undertail-coverts. Sexes very similar; in past, thought to differ in iris colour, slate-coloured in female and white in male, but recent ringing studies indicate that eye colour may be age- and not sex-related; blue carpal area more prominent in male, though of little use for field identification. Juvenile with short bill, dull

green back, grey or pink bib, entirely pale grey underparts, and brown eyes; lacks colourful pink, blue and yellow patches of adult.

**Habitat.** Ecologically adaptable. Commonly found in xeric, mesic, wet and riparian woodland, thickets, deciduous and semi-deciduous forest, pine (*Pinus caribaea*) forest and secondary vegetation, and on mountain slopes; especially partial to gulleys. Frequents grapefruit orchards on I of Pines. Only tody to inhabit shoreline habitat, primarily inland of sea-grape (*Coccoloba uvifera*) thickets. Highest recorded altitude 1974 m, in Pico Turquino. In coastal and subcoastal xeric and semi-deciduous habitats, 0.35-1.6 captures/100 net-hours.

**Food and Feeding.** Primarily insectivorous. Recorded prey include caterpillars, small adult and larval insects, a coreid bug (Hemiptera), sphinx moths (Sphingidae) and flies (Diptera); also spiders, occasionally small lizards; also, rarely, small fruits. Feeds by fly-catching off leaves, main technique the "Underleaf-sally"; also takes insects in mid-air. In arid scrub, mean foraging height 2.6 m.

**Breeding.** Season Mar/Apr-Jun. Excavates burrow c. 30 cm long in earth bank, rotten log, or occasionally at cave entrance, on Cayo Coco also in sand at entrance of crab burrow; sometimes uses natural cavity in limestone; burrow reportedly with thick sticky covering of algae, grass, lichens

and other material. Usually 3 eggs, sometimes 4; eggs smallest of all todies, average 15.5 × 12.6 mm. No further information available.

**Movements.** None recorded.

**Status and Conservation.** Not globally threatened. Widespread and locally common, especially in gulleys. In 1970, common in protected Guantanamo Naval Base, from sea-level up to 130 m. Cuba's relatively low rate of deforestation and many areas of protected forest suggest that populations are quite secure; human poverty, possibly on increase, could pose threats for future. On Cayo Coco, recent aerial spraying and "fogging" with Malathion to control the mosquitos and sandflies that constitute a menace to rapid tourist development, could be reducing this species' populations.

**Bibliography.** Allen (1961), Anon. (1998d), Barbour (1943), Bond (1985), Danforth (1935), Daniel (1902), Faaborg (1985), Garcia (1980), Garcia & Rojas (1997a, 1997b), Garrido (1980), Garrido & Garcia (1975), Garrido & Kirkeconnell (2000), Garrido & Schwartz (1968), Godínez & Blanco (1995), González-Alonso *et al.* (1992), Hernández, D. *et al.* (1999), Hernández, Y.C. & Pérez (1997), Kepler (1972, 1977), Mancina & Garcia (1997), Raffaele *et al.* (1998), Ricklefs & Bermingham (1997), Rolle (1960), Stotz *et al.* (1996), Todd (1916), Walkinshaw & Baker (1946), Wallace (1995), Wallace *et al.* (1996), Wetmore (1932).

#### 2. Broad-billed Tody *Todus subulatus*

**French:** Todier à bec large **German:** Breitschnabeltodi **Spanish:** Barrancoli Picogruoso  
**Other common names:** Hispaniolan Tody

**Taxonomy.** *Todus subulatus* G. R. Gray, 1847, no locality. Monotypic.

**Distribution.** Hispaniola, including Gonâve I.



**Descriptive notes.** c. 11.5 cm; c. 7-7.5 g (Gonâve specimens slightly smaller than those of main island). Largest of the todies. Bright green above, with conspicuous yellow-green lores and supercilia, and a few grey feathers below ear-coverts; red throat, with rest of underparts greyish-yellow, but pink on flanks; iris slate-coloured; bill broad, upper mandible black, lower red. Very similar to *T. angustirostris*, differing in slightly larger size, more iridescent green dorsally, yellower below, more pink on flanks, slate (not white) iris, and no black tip to lower mandible; normal behaviour is less active. Sexes alike. Juvenile

with short bill, dull green back, grey or pink bib, much grey on breast; lacks pink and yellow patches of adults.

**Habitat.** Primarily arid and semi-arid, lowland scrub-forest and subdesert dominated by leguminous trees (*Mimosa*, *Cassia*, *Acacia*), microphyllous shrubs such as lignum-vitae (*Guaicum officinale*) and gumbo limbo (*Bursera simaruba*), cacti (*Cephalocereus*) and agaves (*Agave*); also lower montane forest, second growth, shaded coffee plantations, pine forest, humid ravines; occurs

in mangroves on Samana Peninsula; very rarely in dense rainforest; from depressions 40 m below sea-level up into highlands, at 1750 m and above. Range overlaps with that of *T. angustirostris* at higher elevations in some mountain ranges.

**Food and Feeding.** Insects. Foraging habits typical of genus; main technique the "Underleaf-sally". Of all todies, is the most adapted to xeric conditions; mean foraging height 2.3 m in xeric scrub, 5.3 m in rainforest. Resource-partitioning strikingly evident where occurs alongside *T. angustirostris*: e.g. average foraging height 3.1 m where latter absent, but when sympatric 5.2 m and then, compared with *T. angustirostris*, feeds higher up, makes longer and fewer flights, takes larger prey, and activity slower.

**Breeding.** Breeds Apr-Jun. Digs burrow 30 cm or more long, longest 47.3 cm and 60.0 cm, with average width 3.7 cm and height 4.0 cm, in steep-sided bank or occasionally in steep-banked drainage ditch of sisal field; average height above ground 1.0 m. 3-4 eggs; eggs the largest of all todies, with average size 16.9 × 14.3 mm. No further information available.

**Movements.** None recorded.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in Hispaniola EBA. The more abundant of the two *Todus* species in Hispaniola. No recent detailed information available on numbers, but appears common to locally abundant over most of range, especially in lowlands. Populations possibly diminished owing to habitat destruction, predation of burrow contents by mongooses (*Herpestes*) and humans, and increase in non-shaded, as opposed to shaded, coffee plantations.

**Bibliography.** Anon. (1998d), Bond (1928, 1985), Christy (1897), Curzon (1998), Danforth (1929), Dod (1987, 1992), Faaborg (1985), Kepler (1972, 1977), Latta & Wunderle (1996a, 1996b, 1998), Raffaele *et al.* (1998), Ricklefs & Bermingham (1997), Rutgers & Norris (1977), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wetmore & Lincoln (1933), Wetmore & Swales (1931), Wunderle & Latta (1996).

### 3. Narrow-billed Tody

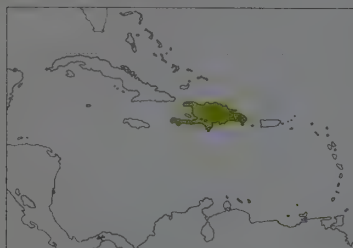
#### *Todus angustirostris*

**French:** Todier à bec étroit **German:** Schmal Schnabeltodi **Spanish:** Barrancoli Picofino

**Taxonomy.** *Todus angustirostris* Lafresnaye, 1851, Hispaniola.

Prior to 1851, considered synonymous with *T. subulatus*, the two forms thought to represent male and female of same species. Monotypic.

**Distribution.** Hispaniola.



**Descriptive notes.** c. 11 cm; c. 5.2-6.7 g. Brilliant green above, with pale green supercilia, and a few grey feathers on lower cheek; red throat, whitish breast and belly, pink flanks, yellow vent; iris whitish; upper mandible black, lower red, usually with blackish tip. Rather similar to sympatric *T. subulatus*, but differs in whitish (not yellowish) belly, also narrower bill with lower mandible usually blackish distally, and iris whitish (not slate-coloured); behaviour is generally more active. Juvenile has short bill, dull green dorsal plumage, grey or pink bib, and considerable amount of grey on breast; lacks the colourful

pink and yellow patches of adult.

**Habitat.** Primarily dense, wet montane forest with canopy of 6-9 m, thickly covered with epiphytic mosses, leafy liverworts, orchids, Spanish moss, ferns, and climbing, razor-sharp bamboo grass (*Arthrostylidium*); also commonly ravines in dry lower montane forest, pine (*Pinus occidentalis*) forest, and shaded coffee plantations dominated by guaba (*Inga vera*), mango (*Mangifera indica*), avocado (*Persea americana*), citrus (*Citrus*) and plantains (*Musa*); occurs also in unshaded coffee plantations. Found down to sea-level in NE (Samana Swamp forest) and SW Hispaniola (Sierra de Bahoruco), but principally at elevations of 1000-3200 m. Range overlaps locally with that of *T. subulatus* in lowlands and lower montane forest.

**Food and Feeding.** Almost solely insects recorded; very occasionally tiny lizards. Keeps well hidden in thick tangles of dense, vine-laced vegetation, hopping among leaves and twigs in limited flying space; mean foraging method the "Underleaf-sally". Mean foraging height 1.7 m in xeric scrub, 2.7 m in rainforest. Where species occurs with *T. subulatus*, resource-partitioning clearly evident: e.g. mean foraging height 2.7 m where latter absent, but mean 2.3 m where sympatric and then, compared with *T. subulatus*, feeds lower in canopy, with shorter flightpaths, takes smaller prey, and duration of perching between flights is shorter.

**Breeding.** Breeds Apr-Jun. Excavates burrow 30-35 cm long, with average width 4.4 cm and height 3.9 cm, in earthen bank, often in more vegetated site than those used by other todies; average height above ground 3.2 m. Usually 3-4 eggs, sometimes 5; egg dimensions 15.5 × 13.5 mm. No other details available.

**Movements.** Resident; possible short, seasonal movements to lower altitudes in cooler months, returning higher to breed.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in Hispaniola EBA. Formerly listed as Near-threatened. Little recent information on status; the least abundant today, appears to be most numerous in mature broadleaf forest in the humid uplands. Populations expected to diminish further owing to habitat destruction, which is particularly rapid in Haiti, and spread of non-shaded coffee plantations, although species will to some degree accept latter habitat. Much predation by mongooses (*Herpestes*), as well as by children, who also kill adult birds with slingshots.

**Bibliography.** Anon. (1998d), Bond (1928, 1949, 1985), Christy (1897), Danforth (1929), Dod (1987, 1992), Faaborg (1985), Kepler (1972, 1977), Latta & Wunderle (1996a, 1996b), Raffaele *et al.* (1998), Ricklefs & Bermingham (1997), Rimmer *et al.* (1998), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Wetmore & Lincoln (1933), Wetmore & Swales (1931), Wunderle & Latta (1996).

### 4. Jamaican Tody

#### *Todus todus*

**French:** Todier de la Jamaïque **German:** Grüntodi **Spanish:** Barrancoli Jamaicano

**Taxonomy.** *Alcedo Todus* Linnaeus, 1758, Jamaica.

Birds trapped at 1200 m significantly heavier and longer-winged than those at 650 m, perhaps subspecifically distinct. Monotypic.

**Distribution.** Jamaica.



nile with short bill, dull green back, grey or pink bib, much grey on greenish-washed breast; lacks the colourful blue-green and yellow patches of adult.

**Habitat.** Widespread in wet, mesic and dry forest; most abundant in wooded hills and mountains. In one study, preferred habitat reported as primary and secondary woodland such as mangrove, dry lowland forest, hill forest, mistforest at medium elevation, becoming rare above 1500 m in the Blue Mountains and not observed on the ridge there; not recorded in pine plantations.

**Food and Feeding.** Insects and their larvae, also occasionally fruit. Foraging habits typical of family, using mainly "Underleaf-sally". Usually forages in understorey, 1-5 m above ground; mean foraging height 2.9 m in xeric scrub, 5.2 m in rainforest.

**Breeding.** Breeds Dec-Jul. Burrow with mean height 3.9 cm, mean width 3.5 cm, dug in vertical earth bank, vegetated or not, at average height above ground of 1.3 m, in limestone habitats, burrow close to ground or in narrow soil layer overlying rocky outcrop; also noted excavating in dead wood, and nest once found in cleft in stone wall. 1-4 eggs, average clutch size 2.8; egg dimensions 16.1 × 13.3 mm. No other details available.

**Movements.** No movements recorded.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in Jamaica EBA. Reportedly widespread and common, from coastal areas to mountains, but little recent information on status. Linear densities/km range from 0.6 in montane rainforest and 4-14 in dry limestone forest to 16 in wet, mesic limestone forest. In one study, density found to be highest at trapping site at 1200 m, but perhaps because soil there loose and very suitable for burrowing. Populations expected to be diminishing as a result of habitat destruction and through predation by mongooses (*Herpestes*) and rural children.

**Bibliography.** Anon. (1998d), Attewell (1907), Bond (1985), Danforth (1926), Diamond (1974), Douglas (1996), Downer & Sutton (1990), Faaborg (1985), Gosse (1847), Griswold (1959), Kepler (1972, 1977), Lack (1976), Raffaele *et al.* (1998), Ricklefs & Bermingham (1997), Salmon (1967, 1971), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Sutton (1973), Witt, Schuchmann & Sutton (1981), Witt, Sutton & Schuchmann (1983).

### 5. Puerto Rican Tody

#### *Todus mexicanus*

**French:** Todier de Porto Rico **German:** Gelbflektentodi **Spanish:** Barrancoli Puertorriqueño

**Taxonomy.** *Todus mexicanus*, Lesson, 1838, Tampico and Vera Cruz, Mexico; error = Puerto Rico. Monotypic.

**Distribution.** Puerto Rico.



**Descriptive notes.** c. 11 cm; male c. 5.5-7 g, female 5.6-5.5 g. Smallest-bodied and least colourful of the todies. Bright green above, with small blue carpal patch inconspicuous in field; few grey feathers on lower cheek; red throat, whitish breast (often streaked or washed grey), yellow belly and flanks, with no pink; iris slate-coloured; upper mandible black, lower red. Female like male, but carpal patch duller, iris white. Juvenile has shorter bill, pale grey bib, yellowish belly; 4 maturation stages each of up to c. 3 weeks, during which bill lengthens to adult size, bib becomes pink, then red, belly whitens, and

bright yellow flanks develop.

**Habitat.** Found in wide range of habitats from rainforest to arid scrub and dense thickets, shaded coffee plantations, mesic forest and karst landscape, often near streams. From coastal lowlands to hills and mountains.

**Food and Feeding.** Insectivorous, with 14 orders and 49 families identified: over 50% of diet consists of flies (Diptera) and beetles (Coleoptera); also lanternflies and leafhoppers (Homoptera), earwigs (Dermaptera), moths and butterflies along with their caterpillars and pupae (Lepidoptera), wasps etc. (Hymenoptera), grasshoppers, crickets and palmhoppers (Orthoptera), stick-insects (Phasmida), praying mantises (Dictyoptera), damselflies (Odonata), and lacewings (Neuroptera), as well as insect eggs. Also spiders, nematodes, millipedes, small lizards (*Anolis*), and fruits from 6 plant families (principally genera *Ficus*, *Chenopodium*, *Rubus*, *Xanthoxylum*, *Psychotria*, *Bocconia*, *Brunellia*, *Clusia*). Prey ranges from almost microscopic to moths and damselflies 5 cm long. Adults select size and variety of nestling foods, especially during first 6 days. One recent study reported nestlings at one nest being brought fruit in 18% of 163 feeds by adults; only 1 species, the small fruits of the tree *Clusia krugiana* (Guttiferae), was fed to the young. Typically, feeds by fly-catching off leaves or in mid-air; main technique the "Underleaf-sally". Mean foraging height 2.1 m in xeric scrub, 4.7 m in rainforest.

**Breeding.** Most-studied todid species. Burrows excavated Sept-Jun, especially Feb-May; laying Mar-Jul. Individual burrows require 2 months to complete; tunnel horizontal, almost always with right-angled curve (equally divided between left and right), with enlarged, depressed, unlined, terminal chamber; entrance of completed burrow near-circular, on average 3.6 cm (2.5-5 cm) high and 3.4 cm (2.5-5 cm) wide; average burrow length in rainforest 30.5 cm (12-58 cm), in xeric scrub 26.9 cm (12-38 cm); built in earthen bank, with mean height above ground 0.9 m in rainforest, 0.5 m in xeric scrub. 1-4 eggs (mean 2.4), but nests with additional helpers have significantly larger clutches (mean 2.9) than those without (2.3); eggs average 16 × 13.5 mm, each one 26% of female's body weight; incubation 21-22 days; chicks altricial, brooded infrequently, nestling period 19-20 days; fledglings emerge with short bill and grey bib, fed for 3 weeks after leaving burrow, and take 42 days to acquire adult morphology.

**Movements.** None recorded.



**Status and Conservation.** Not globally threatened. Restricted-range species: present in Puerto Rico and the Virgin Islands EBA. Generally considered to be common and widespread. Recorded linear densities include: 0-28 birds/km in montane rainforest; 13-31 birds/km in coffee plantations; 3-36 birds/km in dry limestone forest; 10-20 birds/km in wet, mesic limestone forest; and 0-30 birds/km in second growth and riparian woods. No recent detailed information on status. Populations expected to be diminishing as a result of habitat destruction and increasing tendency towards use of non-shade coffee plantations. Observations indicate that introduced Indian mongoose (*Herpestes auropunctatus*) destroys over 80% of nests in rainforest, but only 6% in dry forest; eradication of the mongoose is highly desirable, but is currently considered impossible to achieve on such a large

island. Puerto Rico was badly hit by Hurricane Georges in Sept 1998, but a subsequent study revealed no signs of any major population decline in present species; interestingly, however, birds adapted to forage at lower average heights than previously, although main foraging techniques remained unchanged.  
**Bibliography.** Anon. (1998d), Biaggi (1983), Bond (1985), Faaborg (1985), Faaborg & Arendt (1995), Hernández (1999), Kepler (1972, 1977), Merola (1995), Merola-Zwartjes & Ligon (2000), Odum & Pigeon (1970), Oniki (1975), Otero-Vázquez (1998), Pérez-Rivera & Dechoudens (1996), Raffaele (1989), Raffaele *et al.* (1998), Reagan & Waide (1996), Recher (1965), Recher & Recher (1966), Ricklefs & Bermingham (1997), Rolfe (1963), Statlersfield *et al.* (1998), Stotz *et al.* (1996), Wetmore (1916, 1927).

Class AVES  
Order CORACIIFORMES  
Suborder ALCEDINES  
**Family MOMOTIDAE (MOTMOTS)**



- Medium-sized arboreal birds, with more or less broad, flattened bill, short, rounded wings and short legs; most with racquet-tipped tail.
- 16-48 cm.



- Neotropical.
- Tropical and subtropical forest and woodland; some species also in semi-open areas.
- 6 genera, 10 species, 47 taxa.
- 1 species threatened; none extinct since 1600.

### Systematics

The historical facts behind the name Momotidae are of some interest. "*Motmot*" was the Mexican name of a bird which Francisco Hernández, in his posthumous 1651 work *Historia Avium Novae Hispaniae*, described well enough as to leave no doubt about the particular bird to which he was referring. Soon afterwards, the name was printed as "*Momot*" by Nieremberg and others, and this gave rise to the Latinized *Momotus*, the genus erected by Brisson in 1760. Its "barbarous" origin, however, induced Illiger, a nomenclatural purist, to substitute for it in 1811 the name *Prionites*, and this name was used by many writers in the following decades, until it was sensibly recognized that valid generic names need not be of Latin or Greek origin. It is appropriate that the name now used for the family is based on a native name from Mexico, the country that, along with neighbouring Guatemala and Honduras, is home to the largest number of motmot species.

With only ten species, as currently recognized, Momotidae is one of the smaller groups in the diverse assemblage of coraciiform birds which resulted from the early radiation, probably in the Eocene, of arboreal perching birds. The family is almost certainly monophyletic. Within the Coraciiformes, all the available evidence suggests that the motmots are most closely related to the bee-eaters (Meropidae), kingfishers (Alcedinidae) and todies (Todidae). They appear to be closest to the Todidae, with which some authors have united them in a superfamily. These four families are characterized by the peculiar form of their middle-ear ossicles, as well as by details of limb musculature, and their grouping together is supported by the DNA-DNA hybridization studies undertaken by C. G. Sibley and J. E. Ahlquist. In his comprehensive 1999 review of avian evolution, A. Feduccia recognizes them informally as "alcediniiform". In appearance and behaviour, all four share a number of features: they have bright plumage, the sexes are generally alike, they capture prey mainly by aerial sallies, and they nest in excavated burrows or holes without adding nest material. A fifth family, the trogons (Trogonidae), exhibits much the same characteristics, and is sometimes considered to be closely related to the Momotidae, but the Trogonidae are more clearly sexually dimorphic.

A motmot-like Oligocene fossil from Switzerland, *Protornis*, suggests that the ancestral motmot originated in the Old World. Further evidence of an origin in the Northern Hemisphere is provided by the discovery in Florida, in the southern USA, of a fossil motmot from the late Miocene, which pre-

dates the land connection between North and South America. Judging from the proximal end of a humerus, of distinctive shape and different from that of all other coraciiform birds, this latter was morphologically quite close to living motmots. Feduccia concludes that, in the late Tertiary, a combination of climatic deterioration and competition with other, perhaps more efficient, lineages entirely eliminated the tody/motmot assemblage from the Old World. The same climatic change probably restricted the early motmots to tropical or subtropical Central America; then, with the formation of the Central American land-bridge, about 2.5 million years ago, they spread to South America. There, they apparently underwent little further radiation, and the Momotidae is now the only avian family with its centre of diversity in Central America.

Indeed, not only did the motmots that penetrated into South America not diversify much, but they also achieved a rather incomplete colonization. Only the genus *Momotus* became very widespread, while *Electron* and *Baryphthengus*, apart from the unlikely possibility that they later became extinct there, failed to colonize the huge forest area north of the Amazon, in Venezuela,



Living high in the Andes, the Highland Motmot has often been treated as no more than a high-altitude representative of the Blue-crowned Motmot (*Momotus momota*). While the two appear to be closely related, they exhibit considerable differences in ecology, as well as lesser ones in plumage, and size. These differences appear sufficient to justify the separation of the two forms as full species.

[*Momotus aequatorialis chlorolaemus*, Manu Road, Manu, Peru. Photo: Marc Guyt]



All but one of the motmots have the tail strongly graduated, with particularly long central feathers. The majority of species are further distinguished by the distal part of each of these two central rectrices having the shaft bare, with a peculiar racquet-like tip. This characteristic feature is well shown by this adult Broad-billed Motmot. It is interesting that the racquets are not evident when the feathers are very new, but are created as the weakly attached barbs rapidly wear off or fall away. The function of this curious feature is uncertain, but it may play a part in visual signalling.

[*Electron platyrhynchum minor*,  
Costa Rica.

Photo: Steve Kaufman/  
DRK]

the Guianas and adjacent northern Brazil, and the presence of *Hylomanes* is marginal, reaching only north-west Colombia.

There has long been a good measure of agreement on the recognition of genera within the Momotidae. Two of the six genera are distinctive. These are *Hylomanes* and *Aspatha*, both of which lack the racquet-like tips of the central tail feathers that are the outstanding feature of the four genera of "typical" motmots (see Morphological Aspects). They also differ from the latter in some other plumage features and, in the case of *Hylomanes*, some structural characters. *Hylomanes*, with its subdued plumage, shortish tail, unserrated bill and small size, has generally been regarded as primitive, the little-changed descendant of the early motmots that first colonized Central America. While this may be the case, the opposite interpretation should perhaps also be considered: namely, that *Hylomanes* and *Aspatha* have lost some of the original momotid characters, including the tail-racquets.

At the species level, there are a few points of disagreement or uncertainty. The two species of *Baryphthengus* have often been treated as conspecific. They replace each other geographically, and they are similar in plumage. The eastern one, however, the Rufous-capped Motmot (*Baryphthengus ruficapillus*), lacks the racquet-tipped tail of some, but not all, populations of the more widespread Rufous Motmot (*Baryphthengus martii*); it is also less rufous below, and it is reported to have a different voice. The separation of the two into distinct species is in accordance with many other, similar cases involving closely related allopatric populations. Curiously, but perhaps coincidentally, it is the populations of *B. martii* east of the Andes, thus geographically closest to those of *B. ruficapillus*, that lack the racquet tips to the tail.

Conversely, the Broad-billed Motmot (*Electron platyrhynchum*) has sometimes been treated as constituting two species, one to the west of the Andes and the other to the east of that mountain range. The eastern populations, like those of the Rufous Motmot, lack the tail-racquets. It is quite likely that further research will strengthen the case for recognizing two species, but in the meantime the currently accepted treatment is to unite the populations in a single species. On the other hand, the Keel-billed Motmot (*Electron carinatum*) has traditionally been treated as a separate species from the Broad-billed Motmot. Although the two are very different in plumage, they do nevertheless show a strong structural similarity which suggests a close relationship. Moreover, mixed pairs have been recorded in Costa Rica over two successive seasons, in 1985 and 1986, including apparent courtship feeding of the Keel-billed by the Broad-billed Motmot, and the vocalizations of the two species are reported to be similar. Further study of the taxonomic status of these two motmots would seem desirable.

Some uncertainty exists also with regard to the Blue-crowned Motmot (*Momotus momota*). Those populations in western Panama and the rest of Central America to the west differ in some plumage characters, and perhaps also in voice, from populations to the east, apparently without any intergradation in the area of central Panama where their ranges come close together and may, in fact, meet. This suggests the possibility that the two represent separate species. In addition, the Andean form *aequatorialis*, which is clearly a high-altitude representative and close relative of the Blue-crowned Motmot, has been treated in some recent works as a race and in others as a separate species. Its large size and its considerable differences in plumage, as well as undoubted ecological differences, almost certainly justify its being ranked as a full species, the Highland Motmot (*Momota aequatorialis*).

If the biological species concept, which recognizes subspecies within geographically varying species, were to be rejected, as recently advocated by some taxonomists, in favour of the phylogenetic species concept, then the number of motmot species would be dramatically increased. According to the phylogenetic species concept, every diagnostically distinct population is treated as a full species, and subspecies are not formally recognized. This would mean that, in addition to the cases mentioned above, probably all non-intergrading subspecies of momotids would be given specific status, a treatment which would almost certainly apply to such forms as the isolated Guatemalan subspecies *castaneiceps* of the Russet-crowned Motmot (*Momotus mexicanus*), and the Trinidad and Tobago population



*bahamensis* of the Blue-crowned Motmot. Indeed, the populations of those two islands might themselves be treated as separate species, as detailed examination, especially at the molecular level, would probably bring to light small but diagnostic differences that have developed during the period of their mutual isolation.

This last point is of some interest at the micro-systematic level, bearing in mind the apparent inability of motmots to cross water gaps of any great extent. A difference exists between the length of time over which Trinidad has been isolated from the mainland and the period during which Tobago has been separated from Trinidad. Trinidad was last connected to the South American mainland some 11,000 years ago. Tobago, separated by a much deeper trench, has been an island for far longer, probably about two million years, but the lowering of sea-level at the height of the last glaciation would have reduced the water gap between it and Trinidad to about 10 km or, perhaps, as little as 5 km. It is possible that wind-assisted motmots could have crossed that distance.

At the conventional subspecific level, the main point to note is the need for a re-examination of the validity of the 20 races of the Blue-crowned Motmot, as listed by J. M. Forshaw in his 1987 monograph, as well as of the seven subspecies listed for the Turquoise-browed Motmot (*Eumomota superciliosa*) and the six for the Broad-billed Motmot. None of these taxa has been subjected to thorough recent assessment. In this connection, it is worth noting that a taxonomic review, published in 1991, of the validity of the four subspecies described for the Rufous-capped Motmot showed that all of them were based on individual variation, without any geographical significance.

## Morphological Aspects

The motmots are medium-sized to medium-large arboreal birds, mostly in the weight range 50-150 g. They are large-headed, with a fairly long, stout, slightly decurved bill that varies in width from quite narrow to very broad, with or without a keel-like central ridge, and, except in the Tody Motmot (*Hylomanes momotula*), with serrated cutting edges on both upper and lower mandibles. The serrations vary, too, from being very fine in the Turquoise-browed Motmot and the two *Electron* species to being coarse or very coarse in the genera *Momotus* and *Baryphthengus*; in the case of the last two, the very coarse serrations are perhaps more

accurately described as peaked undulations. There is variation also in the extent of the serrations, which can be confined to the middle part of the bill, as they are in *Aspatha* and *Baryphthengus*, or can extend along most of its length, as is the case with *Electron*, *Eumomota* and *Momotus*. This diversity certainly reflects differences in feeding habits: the species with fine serrations, and also the Tody Motmot with its non-serrated cutting edges, are smaller, and concentrate more on taking flying insects, whereas the larger species, with coarsely serrated mandibles, consume larger prey and more often take their food from the ground (see Food and Feeding). Rictal bristles are well developed, albeit less so in the Tody Motmot, and some of them are strongly recurved.

The legs of motmots are short, and the feet small and weak, with three forward-pointing toes of which the outer two are united as far as the penultimate articulation. The claws are of moderate size, the middle one having the outer edge expanded, but not pectinated. The wings are relatively short and rounded.

The tail consists of ten rectrices in all genera except *Momotus*, which has twelve. In form it is most distinctive. In nearly all species, the sole exception being the Tody Motmot, it is strongly graduated, with the central rectrices much longer than the neighbouring pair and so on down the line to the very short outer pair. Further, in all but three of the species, those being the Tody Motmot, the Blue-throated Motmot (*Aspatha gularis*) and the Rufous-capped Motmot, each of the two central rectrices typically ends in a racquet-like tip, separated from the rest of the feather by a length of bare shaft. An early account of the Blue-crowned Motmot by C. Waterton, in his 1826 book entitled *Wanderings in South America*, alleged that the birds themselves were responsible for this curious and unique tail form, by deliberately denuding the subterminal portion of the feather with the bill. This belief was supported, with further references, by A. Newton in his authoritative *Dictionary of Birds*, published in 1896, and was for long held to be true. The fact is, however, that the barbs are weakly attached along part of the feather near the tip and soon wear off, either in the course of preening or simply through wear and tear.

When first grown by the young motmot, or renewed after a moult, the central rectrices are entire. The racquet tips are ac-

quired as the weakly attached barbs fall away, often not symmetrically on the two feathers, in a process that is quite variable. Thus, A. F. Skutch, in his study of the Turquoise-browed Motmot in Guatemala, recorded that the tail shafts were already bare before the central rectrices were fully grown, this being so both with juveniles still attended by their parents and with a moulting adult on which the central rectrices did not project beyond the lateral ones. J. E. Orejuela, studying the same species in the Yucatán Peninsula of Mexico, found that the distinctive racquet tips had not developed on young birds 20-25 days after fledging, although the central tail feathers showed some wear in the region that was later to become denuded.

The distal portion of the central rectrix, which forms the racquet tip, is wider than the basal portion, more markedly so in some species than in others, and the length of bare shaft varies among different species. The most extreme and spectacular in these respects is the Turquoise-browed Motmot, on which the broad, disc-shaped racquet, twice as wide as the basal part of the vane, along with its long bare shaft, accounts for over half of the length of the tail. It is also noteworthy that in all the racquet-tailed species, apart from the Russet-crowned Motmot and some populations of the Blue-crowned Motmot, the degree of graduation in the length of the tail feathers is such that the tip of the rectrix adjacent to the central one either reaches exactly to, or falls a little short of, the point at which the bare shaft of the central rectrix begins. When the tail is closed, therefore, the racquet tip has its full visual effect.

These facts strongly suggest that the racquet-tipped tail has some function as a visual signal. Nevertheless, none has been apparent in the studies so far carried out, although the pendulum-like side-to-side swinging of the tail is frequently noted. Perhaps it is significant that some populations of the genera *Electron* and *Baryphthengus* do not acquire the racquets, and that, in those which do, the bare portion of the central rectrices is rather short. From this, one could speculate that, in those two genera, the racquet tips were being gradually lost.

In most members of the Momotidae, the plumage coloration is a combination of soft greens, blue and rufous, set off by a striking head pattern that includes black and shining turquoise of various shades, from greenish-blue through blue to violet. In the racquet-tailed species, the racquet itself is basally blue, with the terminal part black, the two colours being sharply demarcated in the Turquoise-browed Motmot, which supports the suggestion of a visual function for the racquet. The black tip is lacking in the species without racquets.

The majority of the species have one or two black spots, or small patches, on the chest. These consist of elongated black feathers, in some species narrowly edged with blue or turquoise, which grow in clusters of at least two big feathers and some smaller ones. The clusters may lie on top of one another, producing a single spot or patch, or they may be separated, producing two spots side by side. The variability of their arrangement, which is affected by preening and perhaps also by other factors, has given rise to conflicting statements in the literature, and requires further study.

Little sexual dimorphism exists within the Momotidae. Males and females of a given species are alike in structure and plumage, but males are a little larger and have a slightly longer tail.

With one exception, the young of those motmots that have been well studied do not have a downy stage. The first feathers to grow are of essentially adult type, but duller in colour, and some elements of the adult plumage, especially the black parts, are lacking. The exception is the Blue-throated Motmot, which breeds high in the Central American mountains. That species' nestlings, clearly as an adaptation to the cold climate, acquire a coat of long, downy feathers which cover nearly the whole body. The down arises from different tracts from those in which the subsequent feathers grow, and so it is not shed from the latter's growing tips, but is pushed aside as the juvenile feathers develop.

The striking similarity in the plumages of the Rufous Motmot and the Broad-billed Motmot has often been remarked on, together with the fact that the ranges of the two species largely overlap. Furthermore, in both species, it is the populations east of the Andes that lack the racquet tips to the tail. All this suggests the possibility of mimicry, perhaps of the kind in which a

Motmots are brightly plumaged birds with a large head, a longish, stout, slightly decurved bill, and short, weak legs. The cutting edges of both mandibles have serrations, these varying from very fine in those species which feed on small insects, to much coarser in those which take larger prey. Among the latter, the very large Rufous Motmot also possesses one or two black spots on the chest, a noticeable character shown by most momotids. For reasons not fully understood, the arrangement of these spots, formed by clusters of elongated feathers, varies within any species, and the marking can appear as a single patch or as two adjacent spots.

[*Baryphthengus martii* semirufus, Barro Colorado Island, Panama.  
Photo: Art Wolfe]





Unlike all other members of the family, the Tody Motmot has a rather short tail with only marginally longer central rectrices, which, moreover, lack bare shafts and racquet tips. It differs further from the others in its much smaller size and chunky build, as well as its more variegated face pattern.

Equally important, although not evident in the field, is the absence of serrations on the cutting edges of the bill, a feature associated with its diet of small insects.

[*Hylomanes momotula momotula*,  
Chan Chich Lodge,  
Belize.  
Photo: R. & N. Bowers/  
VIREO]



smaller species, in this case the Broad-billed Motmot, gains some protection from its resemblance to a larger and more formidable species. Care is needed, however, in arriving at any conclusion, and there is a requirement for at least some evidence, which in this instance is lacking. C. Edelstam, who has discussed all known or likely cases of mimicry of one bird species by another, has pointed out that interspecific resemblance may be simply the expression of a close relationship, or of parallel adaptations to a common environment and shared specializations.

### Habitat

The ten species of Momotidae occur in a wide variety of more or less wooded habitats, from humid evergreen to arid deciduous. Only the Tody Motmot, the Broad-billed Motmot and the Keel-billed Motmot are confined to humid primary forest and older second-growth forest, while the Rufous and the Rufous-capped Motmots live in a wider range of habitats, from primary evergreen forest to semi-open country with tall trees. The most widespread member of the family, the Blue-crowned Motmot, is also the most adaptable in its habitat requirements, occurring not only in primary and secondary forest but also in a variety of man-made habitats, including plantations and even gardens.

The remaining four species are adapted to very different habitats. The Blue-throated Motmot is exceptional in being confined to high altitudes in the Central American mountains, where it lives in temperate evergreen and pine (*Pinus*) forest from about 1500 m to 3000 m above sea-level. The Highland Motmot is restricted to subtropical and lower temperate forest at much the same altitudes in the Andes of Colombia, Ecuador and Peru. At the other extreme, the Central American Turquoise-browed and Russet-crowned Motmots inhabit semi-arid and arid lowlands, in habitats ranging from deciduous woodland to thorn-forest and semi-open areas with scattered trees and hedges.

It is noteworthy that the motmots of the more arid habitats reach levels of abundance far higher than those attained by species inhabiting humid lowlands. Skutch, who has travelled extensively and has almost certainly contributed more than any other naturalist to our knowledge of the breeding habits and behaviour of the Momotidae, has pointed out that motmots are especially abundant in southern Mexico and northern Central America. He states that in that region, especially in the more

open and arid regions, momotids are among the most conspicuous and abundant of birds: "one can not walk far through the thorny scrub and cacti of such districts as the middle Motagua Valley of Guatemala, or the Pacific side of the Isthmus of Tehuantepec, without becoming aware of them." In north-western South America, on the other hand, during almost a year in which he travelled widely on both sides of the Andes, in Peru, Ecuador and Colombia, he did not encounter a single motmot. This may suggest that adaptation to arid habitats is a characteristic of long standing in the motmot lineage, a notion which accords with the evidence that the family spent a long period in Central America before colonizing the generally more humid northern part of South America (see Systematics). In this connection, furthermore, it is perhaps significant that motmots indulge in dust-bathing (see General Habits), a habit found mainly among birds of arid or semi-arid environments.

Whatever their preferred habitat, all motmots require earth banks, either natural or man-made, in which to excavate their nesting burrows. Thus, in primary forest, they tend to be concentrated along ravines and gullies, or along forest paths where these exist. The species that are tolerant of more open, man-altered habitats are often able to make use of roadside banks, or, more exceptionally, the sides of pits or wells or other low structures. Scarcity of suitable nest-sites is an important factor determining local breeding densities. From southern Brazil, there is a report of two occupied burrows of Rufous-capped Motmots situated about 23 m apart. Seven pairs of Turquoise-browed Motmots have been found nesting within a few metres of one another in a railway cutting in Guatemala, and, whereas that species nests solitarily in Costa Rica, it is a colonial breeder in southern Mexico, where it has taken advantage of nest-sites provided by road-building and archaeological ruins (see Breeding, and Status and Conservation).

### General Habits

Motmots are typically rather silent and inconspicuous birds, spending much of their time perched motionless, betraying their presence only by an occasional side-to-side swing of the long tail, or by a sudden dart to seize an insect or other prey. Even the atypical Tody Motmot makes intermittent sideways movements of its comparatively short tail. Occasionally, a bird will stop its



tail in mid-swing, holding it out to the side, perfectly still, for a brief period. It is possible that these conspicuous tail movements have some, as yet unknown, significance in communication. On the horizontal perches which their short legs and small feet oblige them to use for most of the time, they will at intervals turn to face about; as they do so, they give an upward flick of the tail well above the horizontal, thereby avoiding its abrasion against the perch. Their occasional flights are rapid, and usually over short distances. Consequently, it is easy to be unaware of the presence of motmots in the forest or woodland habitats where most of the species live, although this situation normally changes at dawn or dusk, and especially at the start of the breeding season, when their calls may be among the most striking of bird sounds.

The two species that live in more open and arid habitats provide exceptions to that general picture. The Russet-crowned and Turquoise-browed Motmots can be conspicuous, perching freely in the open, even on roadside telephone wires.

Apart from observations made on the Turquoise-browed Motmot, no field studies of momotids have been carried out in which individual birds have been marked. Colour-ringing would, in any case, be less effective than it is for most other bird species, as the short legs of motmots are usually not visible. Nevertheless, it does seem from general observations that adults maintain pair-bonds throughout the year, although this may not be obvious from casual sightings made in the daytime. For instance, the members of a pair of Blue-crowned Motmots often forage separately, but they regularly maintain contact by their calls, which are far-carrying though not loud, and they associate closely together when going to roost in the evening. The detailed studies of the breeding of Turquoise-browed Motmots in the Yucatán Peninsula (see Breeding), using marked birds, showed that pair-bonds are in fact maintained over successive years, as also is fidelity to particular nest-sites.

The nesting burrow, in the excavation of which the male and the female co-operate, is central to a pair of motmots' activities for much of the year. With apparently occasional exceptions, a new burrow is excavated each year, a process that can take several weeks. This work may be undertaken long before breeding begins, at a time when the earth is damp from seasonal rains and is therefore most easily worked (see Breeding). Skutch found that pairs of Blue-throated Motmots begin to excavate a new burrow when their young from the previous breeding season are

independent, and then roost together in it through the non-breeding season, but that Turquoise-browed Motmots use their burrows only in the breeding season, and not as dormitories. His careful observations of Blue-crowned Motmots in Costa Rica showed that the birds do not roost in their burrows, which they excavate long before breeding starts, but that they almost certainly sleep among thick foliage. In Trinidad, however, there is some evidence of pairs of Blue-crowned Motmots roosting in burrows outside the breeding season.

There seems to be no record of motmots bathing in standing water, but the Turquoise-browed Motmot has been seen apparently "bathing" in falling rain. Dust-bathing, on the other hand, has been recorded for the Turquoise-browed, Rufous-capped and Blue-crowned Motmots. As already mentioned (see Habitat), this habit, which is generally associated with birds living in more or less arid country, suggests a phase of adaptation to dry climates in the motmot family's ancestry.

In spite of the striking colour and pattern of the plumage, especially in the head area, and the unique and conspicuous tail structure of most species, such observations as have been made of the social and sexual behaviour of motmots provide no evidence that these morphological features play an important part. In what is apparently courtship behaviour, Blue-crowned Motmots regularly pluck and hold in the bill a leaf or leaves, or twigs and other inedible objects, which, as Skutch remarks, is surprising in view of these birds' complete lack of the use of nest material. In Trinidad, R. French records a group of up to ten individuals all holding leaves or twigs in the bill. During the pre-breeding and breeding period, courtship feeding, apparently not associated with any special display, has been recorded for at least three species, the Turquoise-browed, Broad-billed and Blue-crowned Motmots. Paired individuals regularly call together, in unison or duet (see Voice), this behaviour doubtless assisting in the year-round maintenance of the pair-bond.

## Voice

The commonest call of the Blue-crowned Motmot is a soft, deep, usually double hoot, which has been variously transcribed as "whoo-hoop", "hoo-doot", "hoop-hoop" and so on. Since that species is much the most widespread of the Momotidae, this call will normally, for the casual observer, be his or her first encounter with a motmot. Indeed, it will often be the only encounter, as the low-pitched call carries well through forest or more open woodland, and the caller is likely to be perched motionless and inconspicuous.

The main calls of the two very large motmots, the Rufous and the Rufous-capped, are also soft hoots, whereas the calls of the smaller species are rather different. Thus, the Tody Motmot's call is described as a far-carrying, resonant "cwa-cwa-cwa-cwa...", or a steady, slightly ringing "wok wok wok..." or "wah wah wah...", often prolonged, and given at a rate of about ten calls in 10-12 seconds, or at times faster, ten calls in 3-6 seconds. The primary call of the Broad-billed Motmot is a loud, harsh croak, also described as a nasal resonant "oonk" or "quoonk", uttered singly or in longer series. The main call of the Turquoise-browed Motmot is a deep, throaty "cawak cawak", almost invariably two in succession. A more vivid idea of this last vocalization was given by R. Owen, in one of the earliest accounts of the species; he described it as resembling the laboured expiration of air by a sufferer from whooping cough, and he mentioned the bird's local name of *torovoz* (bull-voice).

Perhaps the most accomplished vocalist in the family is the Blue-throated Motmot of the temperate Central American highlands. Its call is described as a single, far-carrying "hoot" or "huuk", usually repeated every few seconds; it also emits a rapid yodelling series of usually 10-20 hoots, "hoodloodloodlood...", which may involve duetting. The latter is evidently the dawn song which Skutch, in the first of his papers on the life histories of motmots, described as "a deliciously mellow piping, full and round and clear, an undulatory call that carried far across the dim woods and frost-whitened meadows... incomparably more musical than the call of any other motmot I have heard". Skutch

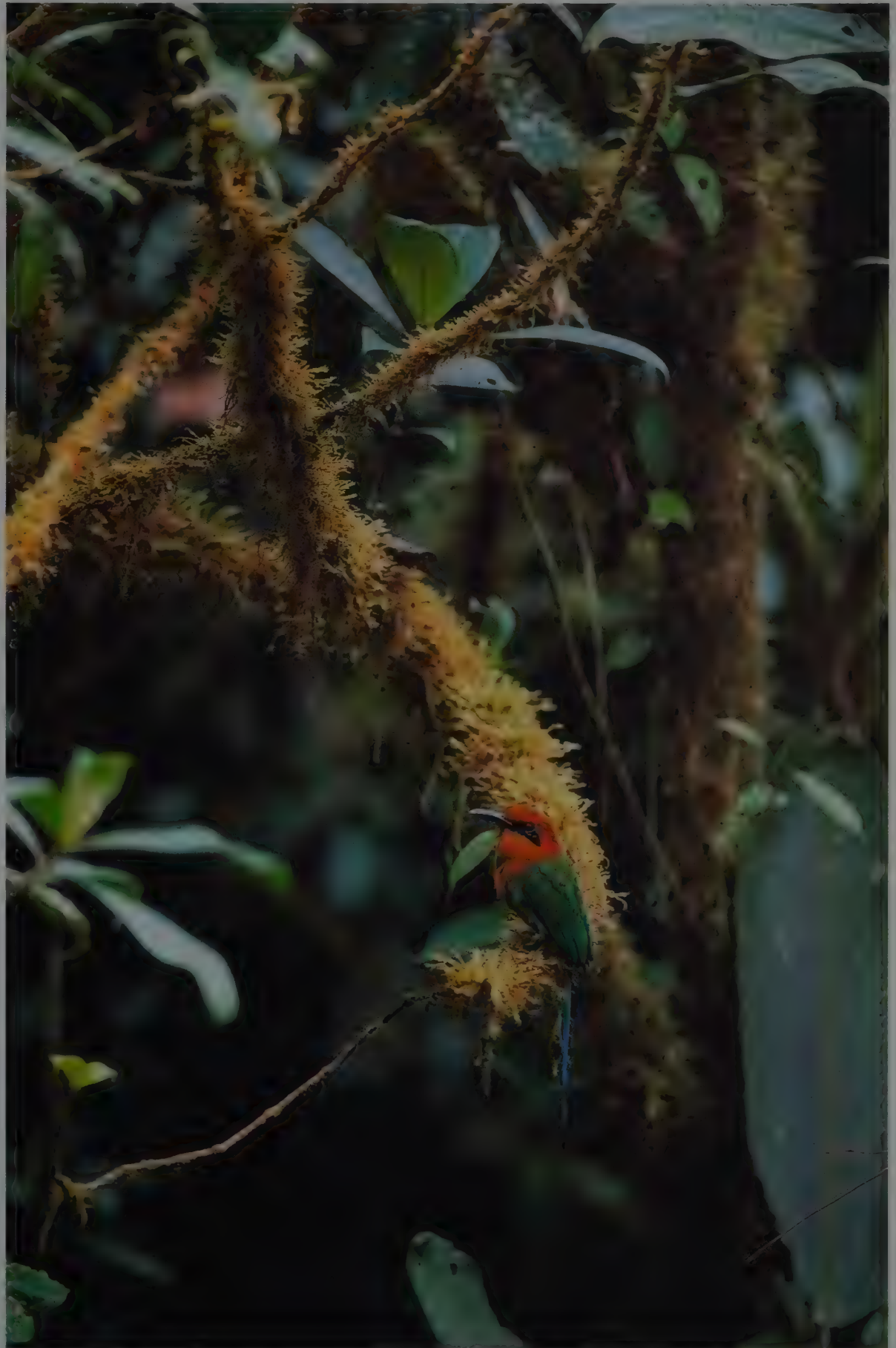
*Little seems to be known about the general habits of motmots, most of which tend to be difficult to observe in their mainly forested habitats.*

*This Blue-crowned Motmot appears to be sunning while resting on a perch, the feathers ruffled to allow the sun's rays to penetrate; this behaviour has not been fully documented for this family, and is probably rather rare in occurrence. The Blue-crowned Motmot is one of three momotids which are known to dust-bathe, but bathing in standing water remains unrecorded.*

[*Momotus momota bahamensis*, Tobago.

Photo: William S. Paton/ Planet Earth]





The members of the Momotidae are found in various more or less wooded habitats, where they require earthen banks in which to excavate their nests.

While several of them extend their spheres of influence into semi-open country, most are more frequently found in relatively thick forest, ranging from evergreen to deciduous and from humid to arid. Three of the ten species are confined to humid primary forest and older second-growth woodland, the Broad-billed Motmot being one of these. It occurs from the lowlands and foothills up to about 1100 m.

This species bears a striking similarity in plumage to the Rufous Motmot (*Baryphthengus martii*), and the two have largely overlapping ranges, a situation made more intriguing by the fact that, in both species, the populations living in forested areas east of the Andes lack the racquet tips to the tail that are such a notable feature of those elsewhere in their ranges. This remarkable similarity between the two suggests possible plumage mimicry by the smaller Broad-billed Motmot, whereby it would gain some protection from looking like its larger and more formidable relative.

It is possible, however, that the resemblance may simply reflect a close relationship between the two species. Alternatively, it may indicate parallel adaptations to a common environment.

[*Eaton platyrhynchum*  
*platyrhynchum*,  
 Rio Nambi, Colombia.  
 Photo: Patricio Robles Gil]



usual call of the male Blue-crowned Motmot in southern Mexico is a double "hoot-hoot" and that of the female a single "hoot", a difference which presumably is maintained in their duets.

Motmots are especially vocal at dawn and dusk, and it is no doubt mainly at those times that territory-holding pairs advertise their presence to their neighbours and register the occupation of neighbouring territories. They may begin very early, at first light. For example, Skutch has recorded that in the humid La Selva Forest Reserve, in Costa Rica, Broad-billed Motmots are the first birds to sing in the dawn chorus, and that their calls are rarely heard after sunrise except, sometimes, at the start of the breeding season.

Young motmots call with increasing loudness throughout their time in the nest. The most detailed account has been given by Orejuela, based on his study of Turquoise-browed Motmots in southern Mexico. On their first day after hatching, the chicks uttered a "peep" call; at four to five days the hunger call was a buzz; at nine to 15 days loud "rattling" hunger calls were given; and at 19-20 days "kla kla kla" alarm calls were emitted. The rattling calls of large nestlings could be heard 30-50 m away, and similar loud rattling calls are recorded by several observers for nestlings of the larger motmots. Nestling Blue-throated Motmots, on the other hand, utter soft trills, and fledgling Broad-billed Motmots are described as uttering soft, mellow notes that are very different from the croaking calls of the adults.

### Food and Feeding

Motmots are rather uniform in their foraging methods, but they take a wide variety of food. They make sallies from a perch, taking prey from leaves, twigs or branches of trees or other vegetation, and regularly also from the ground, while the smaller species also capture prey in the air. They then return to, usually, the same perch, where the prey item, if small, may be swallowed whole at once or, if large, is repeatedly beaten against the perch before being swallowed. Fruits, which are similarly plucked in aerial sallies from a perch, are a regular component of the diet of most momotids, especially the larger ones. The majority of the species that have been well studied have been recorded among the mixed bird parties that accompany foraging army ants, taking the insects and other animals that the ants disturb.



A good example of a momotid that occupies drier habitats is the Russet-crowned Motmot. One of the smaller members of the family, it lives in arid to semi-arid woodland in Central America, extending into semi-open areas with trees and hedges, and reaching elevations of up to 1800 m. Observations show that motmots in more arid habitats generally attain higher levels of abundance, and are notably more conspicuous, than those living in more humid environments.

[*Momotus mexicanus saturatus*, Puerto Arenales, western Chiapas, Mexico. Photo: Daniel F. Lane]

Rather limited in their vocabulary, the motmots utter simple hooting, cawing or croaking notes from a perch. These function as territorial calls, having good carrying power in forest or more open woodland, as well as across semi-open areas. The primary call of the Turquoise-browed Motmot, an inhabitant of arid lowlands, is a deep, guttural, disyllabic croak, almost always given in pairs of notes, and described by one early observer as sounding like the laboured exhalation of a person suffering from whooping cough.

[*Eumomota superciliosa australis*, Guanacaste Province, Costa Rica. Photo: Kevin Schafer]



The foraging techniques of motmots differ relatively little from one species to another. One of the two main methods entails shallow probing into soft ground, where the bill is also used to flick away leaf litter to expose small concealed prey. Ground-foraging is a regular activity of the Blue-crowned Motmot, which takes relatively large arthropod prey. Its bill, being comparatively narrower and shorter than that of, for example, the Turquoise-browed Motmot (*Eumomota superciliosa*), is also more deeply serrated, and is therefore better suited for dealing with larger insects.

[*Momotus momota bahamensis*,

Asa Wright Nature Center, Trinidad.  
Photo: Luiz Claudio Marigo]



The animal prey consumed by motmots consists mainly of large or medium-sized insects, especially beetles, but a great variety of other invertebrates is included, along with some small vertebrates. The only comparative study of the diets of two co-existing motmot species is that carried out by Orejuela, on the Turquoise-browed and Blue-crowned Motmots in the Yucatán Peninsula of southern Mexico. Orejuela found that the smaller Turquoise-browed Motmot preferred smaller insects, which it took mainly in flight, whereas the Blue-crowned Motmot took mainly larger arthropods, many of them from the ground. Dragonflies and Diptera were recorded in the diet of the former species, but not in that of the Blue-crowned Motmot. The differences in bill structure between these two species doubtless reflect adaptations to such dietary differences. The Turquoise-browed Motmot's bill is wide, is finely serrated on the cutting edges, and is relatively longer, whereas the Blue-crowned Motmot's bill is relatively shorter, narrower and deeply serrated, being suited for handling large insects and for crushing hard prey such as molluscs.

The foraging habits of these two momotids also differed. Turquoise-browed Motmots preferred to use "sit-and-wait" tactics, waiting on a perch until a moving prey came close, and then making a quick sally or a short pursuit to capture it. Blue-crowned Motmots ranged more widely; they would exploit several patches, each for a brief period, making rapid and direct flights between them.

Of the non-insect animal food eaten by motmots, the variety is surprising, this being especially so in the case of the larger motmots of the genera *Baryphthengus* and *Momotus*. A Rufous Motmot in Costa Rica has been seen feeding a black-and-green poison-dart frog (*Dendrobates auratus*) to another bird, presumably in courtship. Neither bird appeared to suffer any ill effects, suggesting that the digestive system neutralizes the powerful poison. Rufous Motmots have also been recorded catching small fishes, small crabs, and large scorpions. Blue-crowned Motmots use the bill to probe into soft ground, or to brush away leaf litter to find hidden prey. In addition, they sometimes hop in pursuit of snakes and lizards if those evade their initial pounce from above, and small birds have been recorded among their prey.

As already mentioned, the larger motmots also include a good deal of fruit in their diet. Many kinds have been recorded, and it

is noteworthy that the highly nutritious arillate fruits of the nutmeg family (genera *Virola* and *Compsonera*) and the nutritious fruits of the incense family (*Bursera*), palms, and figs (*Ficus*) are apparently favoured, as they are by more specialized frugivorous birds of medium or large size, such as the toucans (Ramphastidae) and the larger species of cotinga (Cotingidae). In a study of the dispersal of seeds of the nutmeg *Virola surinamensis* in Panama, H. F. Howe found that Rufous Motmots were important agents in this process, accounting for an estimated 17% of all fruits dispersed. In the much drier environment of the Yucatán Peninsula, where suitable fruits are probably less abundant and more seasonal, analysis of stomach contents showed that fruit, by volume, constituted only 3.4% and 8.6% of the diets of, respectively, the Turquoise-browed Motmot and the Blue-crowned Motmot. It should be borne in mind that records of "seeds" in the diet of motmots, either in stomach contents or among the debris found in nests, refer to seeds that would have been, or had been, regurgitated; motmots are not seed-eaters.

The food given to nestlings is much the same as that consumed by the adults. In the case of small young, it is mashed in the parent's bill before being offered, whereas food items are presented whole to larger chicks. Surprisingly, nestling Turquoise-browed Motmots are sometimes fed with lizards, the parents first decapitating the reptiles before squeezing out the soft innards (see Breeding). Fruit is a minor constituent of the food brought to the young of, especially, the large motmot species during the last week or two of their time in the nest. In studies of the Blue-crowned Motmot, the young were 13 days old when they were fed their first fruit.

## Breeding

With the possible exception of the Tody Motmot, which is morphologically atypical and probably primitive, and the nest of which is undocumented, the Momotidae are rather uniform in their breeding habits. They nest in burrows, which are excavated by both sexes, usually in earth banks, and which end in a low, roughly oval-shaped nest-chamber. The clutch is typically of three to five eggs, with extremes of two and six. The eggs, which are white and "short-ovate", in other words nearly spherical, are in-



Food is commonly taken by sallying from a perch towards vegetation, where it is plucked from the foliage or the twigs of trees and bushes. Both invertebrates and fruit are obtained in this way. Animal prey may also be seized when disturbed by army ants. Most motmots that have been sufficiently well studied, such as the Blue-crowned Motmot, have been found at times to join the mixed parties of birds that accompany these insects.

[*Momotus momota lessonii*,  
Las Cruces, Costa Rica.  
Photo: Kevin Schafer]

cubated by both parents, both of which also feed the young. With the single interesting exception of the Blue-throated Motmot (see below), the nestlings lack down feathers, and the feathers which begin to grow a few days after hatching are of adult type, but duller in colour. There is no evidence of nest sanitation. The fledglings are attended and fed by both parents for some days after leaving the nest, although the exact length of the period of dependence has not been determined. After a successful breeding attempt, the burrow is not reused; instead, a new one is excavated, often close by, to be used in the following season.

Breeding pairs of motmots usually nest solitarily. In areas where suitable sites are limited, however, nesting burrows may be concentrated, either in small groups or, in the extreme case of the Turquoise-browed Motmot in southern Mexico, in colonies of up to 100 or more pairs (see Habitat).

When excavating a burrow, the male and the female work in alternating stints. The motmot uses its feet to loosen the earth, which it then kicks backwards as it moves up the tunnel. Earth that has been dealt with in this way, but has not reached as far as the tunnel mouth, is kicked farther back and out of the hole on subsequent visits. Burrows are often by no means straight, but sometimes have bends of as much as 90°, these probably being due to obstructions that prevent forward progress. They can be very long, those of the larger species being up to 3-5 m, and may take several weeks to complete. Burrows which are in active use, or have recently been active, tend to have two parallel grooves along the floor, produced by the movement of the two feet. The burrow entrance is typically wider than it is high, a useful indication of ownership by a motmot rather than by some other bird or mammal. Newly excavated burrows often have a pile of fresh earth below the entrance, making them more conspicuous to potential predators than they would otherwise be, but falling leaves and other debris soon conceal the evidence. Some entrances are, in any case, well concealed behind tree roots, trunks and other objects.

Because of the great difficulty of reaching a motmot's nest-chamber, or even inspecting it without destroying or badly disturbing it, few detailed studies have been made of the breeding behaviour of the members of this family. Those which have been successfully undertaken have been carried out in Central America,

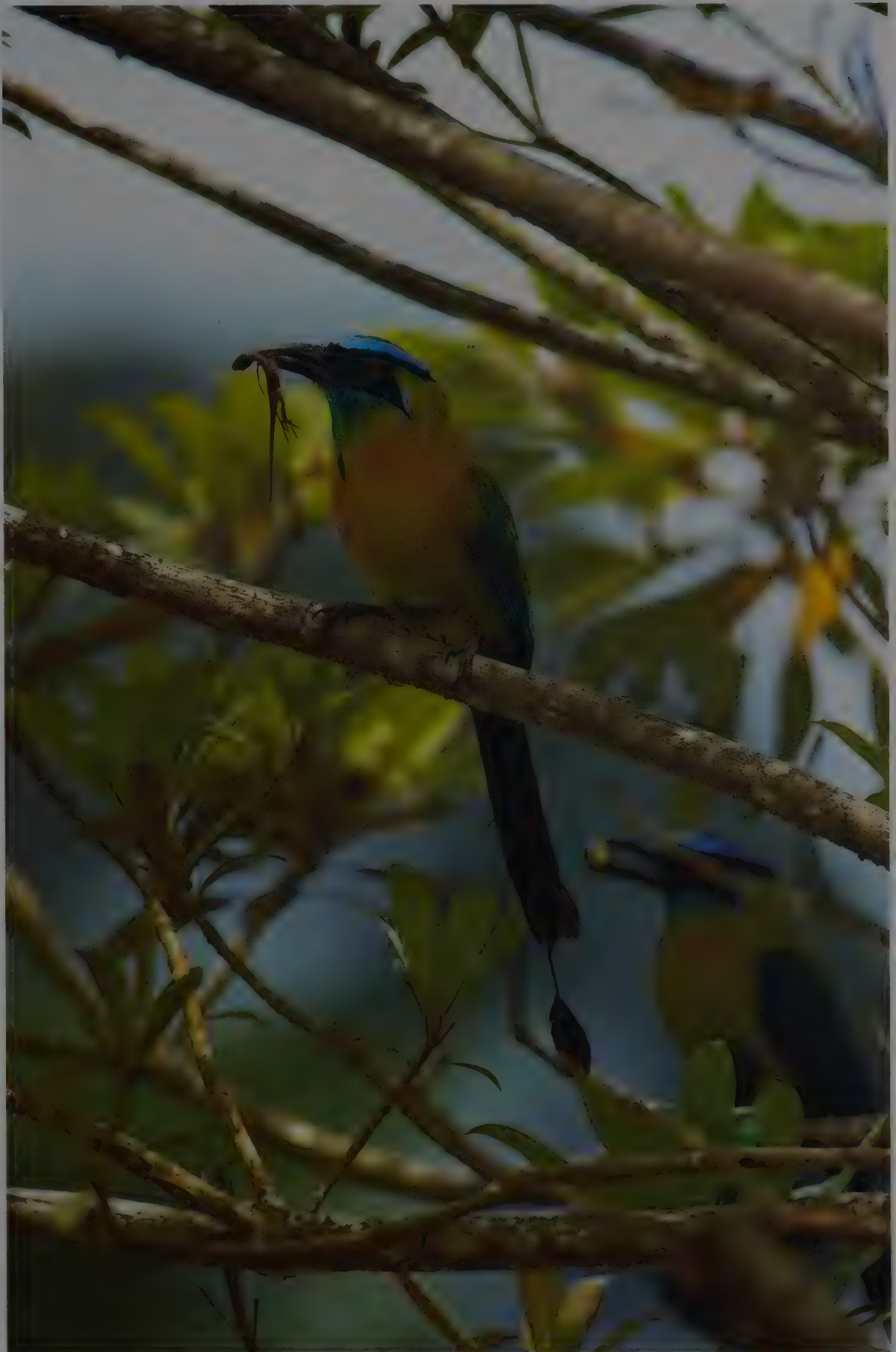
on four species: the Blue-throated, Broad-billed, Turquoise-browed and Blue-crowned Motmots. All four have been among the wealth of tropical American birds studied over many decades by Skutch, while the Turquoise-browed Motmot has also been the subject of a valuable study by Orejuela in the Yucatán Peninsula of Mexico. Shortly thereafter, in the 1980's, again in the Yucatán Peninsula, R. F. and M. W. Martin and P. E. Scott took advantage of the Turquoise-browed Motmot's habit of nesting colonially, and of using existing holes and recesses in Mayan ruins, which are wider and shorter than the burrows excavated by the birds themselves; this enabled them to make a thorough study, and to gather quantitative data on many aspects of the species' breeding biology. Most of the following information is based on the contributions of these few ornithologists.

As already mentioned, it is the rule for a new burrow to be dug for each breeding season. This is clearly a sensible strategy, despite the labour of excavation, since the motmots appear not to practice any form of nest sanitation. The result is that nest-chambers which have contained young often become foul-smelling and crawling with maggots by the time the young fledge, so that their reuse could well be a health hazard to the birds.

All of the four well-studied Central American species breed in the season that is usual for Central American landbirds at latitudes between 10° and 20° N, with egg-laying extending from about March to June and being at its height in April and May. There are, however, marked differences in the timing of burrow excavation. Turquoise-browed Motmots in the Motagua Valley of Guatemala do not start to dig their burrows until the breeding season approaches. Blue-crowned Motmots in southern Costa Rica, on the other hand, often begin to excavate in September or October, finishing the burrows about November, and not using them until four or five months later; the probable reason for this early start is that the ground is more easily workable in the wet autumn season than it would be in the dry season that precedes breeding. Blue-throated Motmots in the highlands of Guatemala begin to dig new burrows even earlier, in June or July, just after their young have fledged. Of the four species studied, this last is the only one that roosts in the burrow through the non-breeding season, doubtless because of the coldness of the nights in its highland habitat.



Although invertebrates probably form the bulk of the food eaten by most motmots, the diet of these birds is remarkably varied. All but the smaller species also take a number of vertebrates, including small reptiles, mammals and, occasionally, small birds and nestlings, as well as regularly consuming a variety of fruits. The Blue-crowned Motmot, the best-known and the most widely studied of all the ten species, not infrequently snatches small lizards from the forest floor, pouncing on the animals from above; it will even pursue in hopping runs any suitably sized snakes and lizards which escape the initial attack. At the same time, this species consumes many fruits when these are available, having a particular liking for those of the nutmeg genus *Compsonera*, among others. With so varied a diet, it is perhaps not surprising that semi-tame individuals in the Caribbean readily accept household food scraps offered to them by humans. There is a degree of uncertainty about the taxonomy of the Blue-crowned Motmot in Central America, where the subspecies from western Panama and westwards, which include *lessonii*, shown here, differ in some plumage traits, in size and, probably, also in voice from those to the east. Since there appears to be no intergradation between them, it is possible that more than one species is involved.



[*Momotus momota lessonii*,  
Monte Verde, Costa Rica.

Photo: Rob Curtis]



Having captured food in an aerial sally, motmots generally return to the same or, less often, another perch to swallow it. It is interesting to note that the young of this family are fed on basically the same diet as that of the adults, although fruit is a far less common food item in the earlier stages. Field studies of the Blue-crowned Motmot revealed that the nestlings were fed on a wholly animal diet until they were 13 days old, at which point they were offered their first fruit.

[*Momotus momota exiguus*, Belize.

Photo: Carol Farneti-Foster/Planet Earth]

The difficulties of gaining access to the nest-chamber have prevented most observers from finding out much about the eggs or nestlings of the members of this family. Moreover, since the burrows so often are not straight, even obtaining a view of the chamber is far from easy. Skutch's solution in a number of cases was to work out, by probing with pliable sticks, where the chamber was likely to be, then to dig down and carefully make an inspection hole in its ceiling; this hole had to be large enough to allow nestlings to be removed for examination, and was plugged with a stone after each inspection. By this means, it was found that there was an interval of five days between the laying of the first and the last of the three eggs of a Blue-throated Motmot, indicating intervals of two or three days between successive eggs; all the eggs hatched over a period of one or two days, showing that effective incubation began with, or shortly before, the laying of the last egg. With the Turquoise-browed Motmot, frequent checks of the more accessible nests, and the marking of each egg as it was laid, revealed that eggs were normally laid at two-day intervals, and that partially effective incubation began with the laying of the first egg, which hatched at least six hours but not more than 24 hours before the second, while the fourth egg always hatched at least 24 hours after the third.

The most detailed study of incubating behaviour achieved by Skutch concerned the Broad-billed Motmot. As is the rule in the family, male and female shared the duty, taking very long stints, with only two change-overs being made in a period of 24 hours. The routine, which for the pair under observation remained unaltered in two successive breeding seasons, was for the probable female to incubate from about noon until before dawn on the following day. After she had left the nest-burrow, following this spell of nearly 18 hours, her mate arrived and entered the hole some 16-45 minutes later. Observation from the burrow mouth showed that the incubating bird had its tail projecting outwards from the nest-chamber into the entrance tunnel, which in that instance was fairly short and straight. This posture is adopted also by the Turquoise-browed Motmot, and probably by all momotid species. Other studies have revealed that incubating Turquoise-browed and Blue-throated Motmots regurgitate the hard parts of beetles and other insects as they sit, until a considerable mass of this animal material forms a bed beneath the eggs.

Accurate incubation periods have been ascertained for only two motmot species. In the cool Guatemalan highlands, Skutch recorded a period of 21-22 days for the Blue-throated Motmot. To the north of there, in the dry lowlands of Yucatán, the marking of eggs and frequent checks showed that incubation periods for single eggs of the Turquoise-browed Motmot were 18-20 days, and that the eggs always hatched in the order in which they were laid.

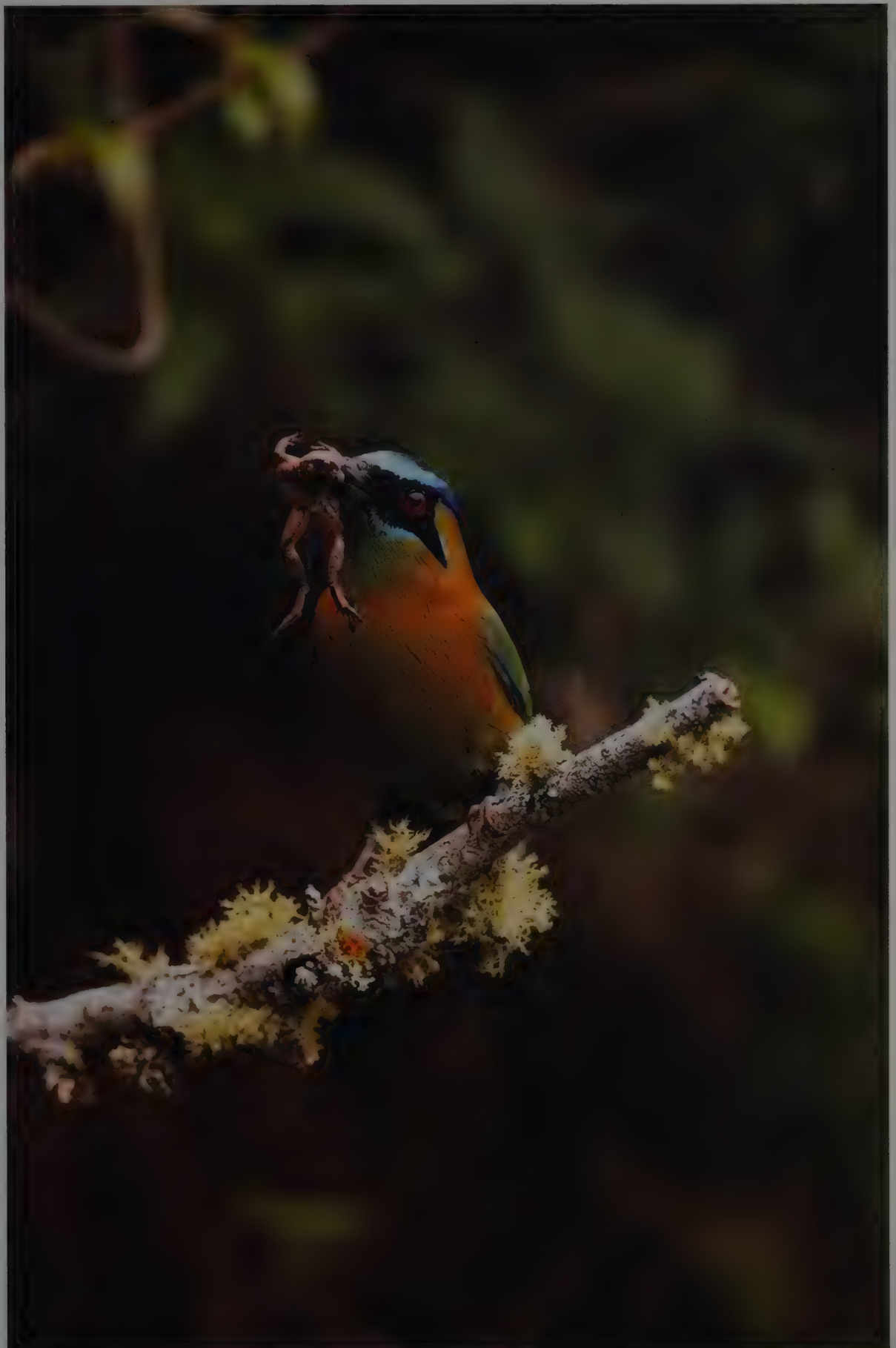
Newly hatched motmots have bare skin, with no trace of down feathers. The most detailed account of their development comes, yet again, from Skutch's study of the Broad-billed Motmot. The nestlings were active as soon as they had hatched, and were able to move around the nest-chamber. Pin-feathers soon began to appear, and at the age of nine days some had already begun to break out of their sheaths; by eleven days the nestlings were partly feathered. The eyelids began to separate at twelve days. On the following day the chicks began to call softly, and thereafter they became increasingly noisy. By the age of 15 days they were taking their food at the burrow entrance, and they left the nest at 24-25 days.

So far as is known, the development of the juvenile plumage from the nestling's bare skin is typical of the family, but the Blue-throated Motmot, breeding in the cool highlands of Central America, is a most interesting exception. Skutch found that the young of that species, soon after hatching, produced long, soft down feathers which almost covered the whole body. This down grew from tracts different from those in which the subsequent juvenile plumage arose. The down was not shed, but was pushed aside as the juvenile feathers developed.

Nestling motmots are fed mainly on insects. In the early stages, these are first mashed up in the parent's bill before being presented, but later they are offered whole. The two parents take an approximately equal share of the brood-feeding duties. Young Turquoise-browed Motmots in the dry Motagua Valley of Guatemala were given a very varied diet, including moths, brilliantly coloured butterflies, and many small insects, but also small lizards up to about 15 cm in length. The adults' method of dealing with these reptiles is somewhat unusual. Skutch wrote that the parents, while in the burrow, and before feeding a lizard to their young, apparently pecked or bit off the reptile's head, and then pressed out the viscera and soft parts through the open neck; on several occasions, he found a lizard's empty skin, almost entire, on the floor of the nest-chamber. Broad-billed Motmots in hu-



Some of the food items captured by, in particular, the larger of the motmot species can be surprisingly big. Of course, any sizeable prey has to be immobilized before being consumed. Vertebrates, such as reptiles and amphibians, are carried back to a perch, where they are repeatedly beaten until dead, and are then swallowed whole. It may seem somewhat remarkable that motmots are able to deal with such comparatively large and unwieldy-looking prey as frogs and snakes, but the task is presumably made easier by the coarse, deep serrations that are present on both upper and lower mandibles. The Blue-crowned Motmot, pictured here in the rainforest of Costa Rica, has a bill powerful enough to deal with good-sized animals. Similarly well equipped is the Rufous Motmot (*Baryphthengus martii*), the largest member of the family; this has even been observed to feed to another of its species a poison-dart frog of the genus *Dendrobates*, with no ill effects suffered by either bird. Nevertheless, although both of these motmot species, as well as several others, are known to attack and kill such prey, it is very likely that the total amount of vertebrate food they take constitutes only a minimal part of the whole diet.



[*Momotus momota lessonii*,  
*lessonii*,  
 Monte Verde, Costa Rica.

Photo: Michael Fogden/  
 DRK]



Like other coraciiform birds, motmots nest in burrows, which both of the pair excavate, generally in earth banks. Typically, motmot burrows have an entrance that is wider than it is high, a feature distinguishing them from the holes made by other birds and by mammals. It is not unusual for a newly dug motmot burrow to have a pile of fresh earth beneath the entrance, but this soon becomes hidden by fallen leaves. In many instances, however, the hole is well concealed behind tree roots, as is often the case with nests of the Blue-crowned Motmot.

[*Momotus momota*, Amazonia, Brazil. Photo: Nick Gordon/Oxford Scientific Films]

mid lowland forest in Costa Rica were seen to be fed almost entirely on insects, supplemented by a few spiders.

In the Blue-crowned Motmot, the adults of which regularly include some fruit in their diet, the young in a nest studied in southern Costa Rica were fed some fruit from the age of 13 days. This was the arillate fruit of *Compsonura sprucei*, a relative of the nutmeg, in which the aril is rich in fats and proteins. Like the adults, the young digested the aril and regurgitated the bare seed.

Nestling motmots become very noisy as they grow older. At the same time, they are remarkably docile. When Skutch removed 20-day-old Turquoise-browed Motmots from a nest in order to photograph them, he noted that their docility, as they perched in a row on a stick, was in striking contrast to the restlessness of Amazon Kingfishers (*Chloroceryle amazona*) at the same age. In his words, "already they seemed to be acquiring a taste for a life devoted largely to motionless contemplation".

The lack of any nest sanitation, as already mentioned, results in the nest-chamber becoming considerably befouled as the chicks grow. Indeed, Skutch, before photographing his nestling Turquoise-browed Motmots, had first to wash the bill and feet of each one as they were so foul; the nest was swarming with maggots. Similarly, he found that the floor of a nest containing large young Broad-billed Motmots was becoming filthy, and teeming with white maggots. Nevertheless, young motmots leave the nest with their plumage immaculate.

In the few species of motmot for which the fledging periods have been accurately recorded, these have in all but one instance ranged from 24 to 32 days. In Guatemala, the nestling periods of both the Blue-throated and the Turquoise-browed Motmots are 28-29 days, while that of the latter in south Mexico has been recorded as 24-31 days. For the Blue-crowned Motmot the period is 29-32 days, with one record of 38 days. There appears to be no detailed record of the length of the parental post-fledging care for any momotid.

Almost certainly, only a single brood is raised in the course of a breeding season. The study of Turquoise-browed Motmots nesting in archaeological sites in the Yucatán Peninsula showed that repeat layings occurred after an initial loss of eggs or small young, and in one case a third clutch was laid after a second failure. These repeat clutches accounted for the few very late dates, in the second half of July, on which egg-laying was re-

corded. The intervals between loss of a clutch or brood and re-laying were ten to 21 days.

## Movements

With their short and rather rounded wings, motmots have a flight that is rapid and dashing, but seldom continuous over long distances. None of the ten species is a long-distance migrant, and for all but one, the Turquoise-browed Motmot, no significant movements have been recorded apart from local ones related to foraging, breeding and roosting.

Motmots are probably unable to cross water of any great extent, and they are present on only two of the islands adjacent to Central or South America, namely, Trinidad and Tobago. As already noted, Trinidad was still connected to the mainland as recently as about 11,000 years ago, in contrast to the two million or so years since Tobago, the outer island, became isolated, but the deep part of the channel between the two islands is narrow, only some 5-10 km wide, and may not have been an insuperable barrier to these birds. It is worth recalling that the Trinidad and Tobago populations of the Blue-crowned Motmot, during their period of isolation, have diverged from adjacent mainland stock to become a fairly well-marked subspecies, with no apparent difference between the populations of the two islands (see Systematics).

Seasonal movements, of unknown length but probably not very extensive, are recorded only for the Turquoise-browed Motmot. In his study of this species in the Yucatán Peninsula, Orejuela found that the birds were absent from the breeding areas in February; they began to return in early March, and the main movement took place within a period of one week. Similarly, at study sites also in Yucatán, Scott and Martin found that, in 1980, no Turquoise-browed Motmots were seen or heard on 23rd and 24th February, but by 18th March the species was conspicuously present. The extent of dispersal away from the breeding areas in the off-season was not determined.

It is possible that seasonal movements are made by Turquoise-browed Motmots in other parts of their range. This is hinted at in the statement by F. G. Stiles and Skutch that, in Costa Rica, the species prefers deciduous woodland and evergreen gallery for-



est, but that it also frequents savanna trees and low scrubby thickets, especially in the wet season.

### Relationship with Man

The motmots, with their unique tail formation and their striking calls, must have been familiar to mankind since his earliest days in the Neotropics. They have a place in some of his legends. For example, H. Sick mentions that one of the legends current among Amerindian tribes in Brazil, and referring to the acquisition of fire by people, explains that the gap in the motmot's tail was caused by the bird's carrying an ember on its tail.

It is not surprising that the hooting call has given the Blue-crowned Motmot a number of local names, such as *houtou* in Guyana and *bouhoutou* in Trinidad. The characteristic call is probably also the origin of the Mexican name *motmot* (see Systematics), which was no doubt pronounced in a different way from the modern English pronunciation.

Motmots are not popular as cagebirds, but some have been maintained in captivity. No doubt the early Mexicans kept them, as they did so many kinds of birds, but the first published record was of a Blue-crowned Motmot held at London Zoo in 1877. This was later followed by instances of several other motmot species being kept in captivity, in various zoos.

Only the Blue-crowned Motmot is recorded as having bred in captivity, for the first time in 1966, and at least three times subsequently. An account of the successful breeding by this species at Kilverstone Wildlife Park, in England, was published by P. F. Larcombe in 1991. At the first attempt, the birds dug into the floor of the aviary, as no earth bank had been provided, and excavated a horizontal burrow only a little below the surface; this tunnel wound about from side to side for a length of 3.4 m, crossing itself several times. When an earth bank was then provided, the pair nested successfully, rearing a total of 13 young over a period of four years.

### Status and Conservation

Since only three species of Momotidae are strictly dependent on humid tropical or subtropical forest, the widespread destruction of such habitats in Central and South America has been less disastrous for them than for some other groups of Neotropical birds. Indeed, one species, the Turquoise-browed Motmot, has actually benefited, at least in southern Mexico, from human activities that

have led to the replacement of primary forest by sparser secondary woodland, a preferred habitat. Moreover, road-building has created abundant nesting sites for that species in roadside banks, while archaeological remains have provided it with another important source of nest-sites. Most strikingly, the ruined masonry of cities and temples now offers a wealth of suitable ready-made holes for colonies of Turquoise-browed Motmots. This has brought an additional benefit to ornithologists, who have been able to take advantage of the accessibility of the nests in order to make quantitative studies of the birds' breeding habits, studies which would hardly have been possible elsewhere (see Breeding).

Although no estimates are available for the number of pairs per unit area, local breeding concentrations of Turquoise-browed Motmots in Guatemala and the Mexican states of Yucatán and Campeche can be impressive. In the Yucatán Peninsula, Orejuela recorded from two to about 30 pairs nesting in close proximity, the number depending on the size of the nesting bank, most cases involving 10-20 pairs; adjacent holes were generally 0.5-2 m apart, but some were separated by as little as 0.3 m. Notably, breeding colonies of more than 100 pairs have been reported from elsewhere in Mexico. In Guatemala, Skutch found seven pairs of Turquoise-browed Motmots nesting within a few metres of one another in a railway cutting. By contrast, in Costa Rica, where the preferred habitat of the species is deciduous woodland and evergreen gallery forest, colonial nesting has not been recorded.

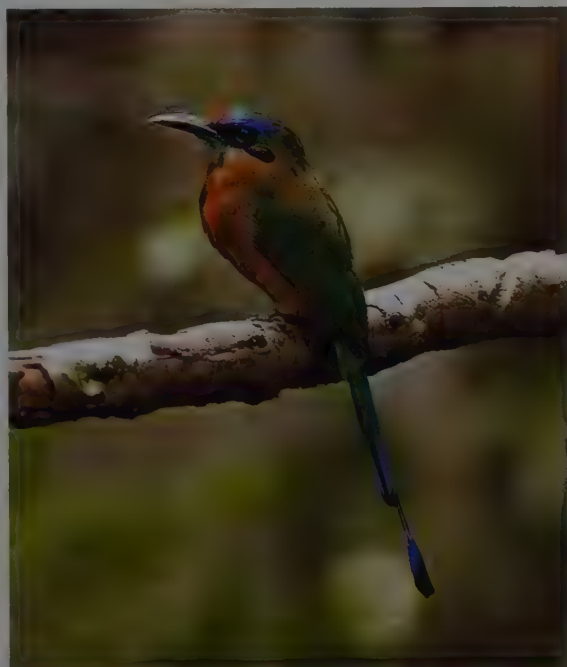
This striking difference between the semi-arid western end of the species' range and the more humid eastern end would surely indicate that higher population densities of Turquoise-browed Motmots can be maintained in more open, drier kinds of habitat, with human activities a positive influence. Orejuela's comparative study of Turquoise-browed and Blue-crowned Motmots in the Yucatán Peninsula showed that the man-made changes favoured the former species at the expense of the latter, the population of which was diminishing as the original high forest on which it depended was progressively destroyed.

The status of those species confined to humid primary or older secondary forest is more difficult to assess, as they are generally inconspicuous and may call little except at dawn and at the beginning of the breeding season. Only one species is classed as threatened at a global level. This is the Keel-billed Motmot, which has a restricted range in Central America from southern Mexico to northern Costa Rica, and is currently listed as Vulnerable. Until recently, it was very poorly known, having been recorded from a rather small number of widely scattered localities. This is not surprising, as early records were all based on collected specimens, and this is the kind of inconspicuous bird that general collectors might tend to overlook.

With the recent great increase in ornithological surveys by experienced observers, particularly since the 1980's, it has become apparent that the Keel-billed Motmot is a good deal more widespread than had previously been thought, and in some areas, especially central and southern Belize, it is reasonably abundant. B. W. and C. M. Miller, who have made long-term studies of the species in that country, consider that Belize probably has the largest known populations of the species. Furthermore, as most of them are within protected areas, their prospects of survival, at least in the short and medium terms, seem good. During a survey in 1994 in the Mullins River basin, the area with possibly the densest population of all, they estimated that 16-20 Keel-billed Motmots were present in an area of 2000 ha. Nevertheless, throughout the rest of the species' range, rampant habitat destruction is leaving populations of this species ever more fragmented, so at present its long-term survival remains in the balance.

### General Bibliography

- Becker (1986), Bock (1994), Burton (1984), Chapman (1923), Cracraft (1981), Feduccia (1999), Forshaw & Cooper (1987), Gaumer (1881/82), Howe (1993), Larcombe (1991), Lowe (1948), Martin *et al.* (1989), Master (1999), Maurer (1978), Maurer & Raikow (1981), Mayr (1998), Miller & Miller (1996), Murie (1872c), Olson, S.L. (1976), Orejuela (1975, 1977, 1980), Peters (1945), Remsen *et al.* (1993), Ridgway (1914), Sanft (1980), Scott & Martin (1983, 1986), Sibley (1996), Sibley & Ahlquist (1990), Sibley & Monroe (1990), Sibley *et al.* (1988), Skutch (1945c, 1947, 1964, 1971, 1985), Verheyen (1955a, 1955b, 1955c), Wagner (1950).



Despite the fact that most motmots live in forest habitats, only one species is considered to be globally threatened. The Keel-billed Motmot, categorized as Vulnerable, has a restricted range from south Mexico to north Costa Rica. Until the 1990's it was known from just a few widely scattered sites, and even ten years later its population remains small and fragmented, with its main stronghold in Belize. One problem for this species is that males in small territories may be unable to attract mates.

[*Electron carinatum*,  
Caracol,  
Cayo District, Belize.  
Photo: Carolyn M. Miller]



PLATE 23

inches 4  
cm 10



## Genus *HYLOMANES*

M. H. K. Lichtenstein, 1839

### 1. Tody Motmot

#### *Hylomanes momotula*

**French:** Motmot nain

**German:** Zwergmotmot

**Spanish:** Momoto Enano

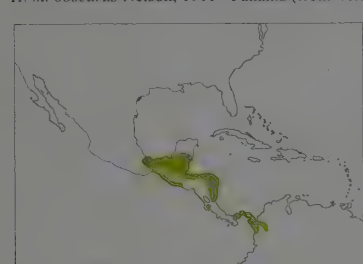
**Taxonomy.** *Hylomanes Momotula* M. H. K. Lichtenstein, 1839, Valle Real, Mexico.

Highly distinctive, with no obvious close relatives; usually regarded as primitive. Geographical variation probably clinal; further study needed. Three subspecies currently recognized.

**Subspecies and Distribution.**

*H. m. momotula* M. H. K. Lichtenstein, 1839 - S Mexico (from S Veracruz and NE Oaxaca) E to extreme E Nicaragua; probably this race in NW Costa Rica (Cordillera de Guanacaste, mainly on Pacific slope).

*H. m. chiapensis* Brodkorb, 1938 - S Mexico (Pacific slope of Chiapas) E to extreme W El Salvador.  
*H. m. obscurus* Nelson, 1911 - Panama (from Veraguas) E to NW Colombia.



**Descriptive notes.** 16.5-18 cm; male 27-33 g, female 25-30 g. Much the smallest motmot, chunky and large-headed; tail shortish with central pair of rectrices only c. 6-7 mm longer than next pair, 3 outer pairs markedly graduated. Both sexes nominate race green crown, rufous nape, blue supercilium, black eye-mask with whitish stripe below; upperparts green, tail all green; tuft of elongated whitish or pale buffy feathers on each side of throat, greenish breast obscurely streaked, belly white; bill black, often paler below at base, rictal bristles rather short and weak; legs and feet brownish to blackish. Differs from all other motmots in small

size, pattern of face and underparts, lack of racquet tips on tail, no serrations on cutting edges of bill. Juvenile duller, with greyish-brown crown and nape. Races *chiapensis* and *obscurus* both darker, latter less white on throat.

**Habitat.** Humid evergreen forest, especially along ravines; to 1850 m.

**Food and Feeding.** Insects, spiders and small snails; butterflies include species of *Morpho*. Unlike most other motmots, not recorded feeding on fruit. Food items plucked from vegetation in flight sallies; butterflies and dragonflies also taken in air.

**Breeding.** Food-carrying adult in Jun and fledgling with adult in early Jul in Belize; fledgling collected in Jun in Guatemala; in Colombia, egg-laying female collected in Feb in NW (Chocó) and female in breeding condition in May in N (Antioquia). Nest unrecorded, presumably in burrow in earth bank. No other details.

**Movements.** None recorded.

**Status and Conservation.** Not globally threatened. Generally local and uncommon throughout its fragmented range; fairly common to common on Atlantic slope from Mexico to Honduras; very uncommon in Costa Rica. Occurs in Tikal National Park, Guatemala. Little known; research required, especially on breeding biology.

**Bibliography.** Anon. (1998d), Binford (1989), England (2000a), González-García (1993), Hernández-Baños *et al.* (1995), Hilty & Brown (1986), Howell & Webb (1995), Land (1970), Lowery & Dalquest (1951), Miller *et al.* (1957), Monroe (1968), Paynter (1955, 1957), Ridgely & Gwynne (1989), Robbins *et al.* (1985), Slud (1964), Siles & Skutch (1989), Stiles *et al.* (1999), Stotz *et al.* (1996), Thurber *et al.* (1987), Vallety & Whitman (1997), Wetmore (1943, 1968).

## Genus *ASPATHA* Sharpe, 1892

### 2. Blue-throated Motmot

#### *Aspatha gularis*

**French:** Motmot à gorge bleue

**German:** Blaukehlmotmot

**Spanish:** Momoto Gorgiazul

**Taxonomy.** *Prionites gularis* Lafresnaye, 1840, Guatemala.

Distinctive, with no obvious close relatives. Has been considered primitive on account of its tail lacking racquet tips. Monotypic.

**Distribution.** S Mexico (from E Oaxaca and Chiapas) through Guatemala and extreme N El Salvador to Honduras.



**Descriptive notes.** 25.5-28 cm; 56-65 g. Tail feathers markedly graduated throughout, no racquet tips; bill with low, well-spaced serrations along middle part of cutting edges of both mandibles, culmen ridged only towards base. Both sexes have side of head ochre-coloured, with black auricular spot; mainly green above, paler green below; tail all dark green, bluer towards tip; throat extensively blue, bordered below by black chest-spot(s); bill blackish, frequently pale straw-coloured below; legs and feet range from straw-coloured to brownish. Differs from other members of Momotidae in

distinctive head pattern, no black eye-mask, pale leg colour. Juvenile duller-coloured head and upperparts, washed olive.

**Habitat.** Humid to semi-humid high montane evergreen and pine forest; 1300-3000 m.

**Food and Feeding.** Mainly insects, especially beetles: some fruit taken, and presumed also fed to young in small quantities, as seeds found among insect fragments in occupied nest-chamber. Insects seized from vegetation in flight sallies.

**Breeding.** Lays in Apr in Guatemala; fledgling collected in second half of May in S Mexico. Nest in burrow excavated in earth bank; burrow often tortuous, with turns of 90° or more, widening at end into oval nest-chamber with low vaulted roof; 4 burrows 1.4-1.8 m in total length. 3 eggs; incubation 21-22 days; nestling, uniquely in family, develops covering of long soft down feathers; fledging 29-31 days.

**Movements.** None recorded; almost certainly very sedentary, as adults attached to burrows (excavating, breeding, roosting in non-breeding season) throughout year. Possibly some altitudinal movement.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in North Central American Highlands EBA. Probably much more abundant than suggested by casual diurnal observations, as species is inconspicuous, and vocal only at dawn; 7 pairs recorded occupying burrows along 1.6 km of winding mountain road in Guatemala. Only low numbers found in upper cloudforest in El Triunfo Biosphere Reserve, in Chiapas, Mexico, where recorded markedly less often in summer, with even fewer in autumn.

**Bibliography.** Anon. (1998d), Binford (1989), Gómez de Silva *et al.* (1999), González-García (1993), Hernández-Baños *et al.* (1995), Howell & Webb (1995), Land (1970), Miller *et al.* (1957), Monroe (1968), Skutch (1945c, 1983), Stattersfield *et al.* (1998), Stotz *et al.* (1996), Thurber *et al.* (1987).

## Genus *EUMOMOTA* P. L. Sclater, 1858

### 3. Turquoise-browed Motmot

#### *Eumomota superciliosa*

**French:** Motmot à sourcils bleus

**German:** Brauenmotmot

**Spanish:** Momoto Cejiazul

**Taxonomy.** *Pyronites superciliosus* Sandbach, 1837, Campeche, Mexico.

Highly distinctive, with no very close relatives. Geographical variation within disjunct range is probably complex, but general pattern of darkest forms in more humid areas, tawnier forms coastal, greener ones isolated in interior, and southernmost distinctly pale; further study required. Seven subspecies currently recognized.

**Subspecies and Distribution.**

*E. s. superciliosa* (Sandbach, 1837) - SE Mexico (from Campeche across N half of Yucatán Peninsula).

*E. s. bipartita* Ridgway, 1912 - S Mexico (Oaxaca, Chiapas) and Pacific slope of Guatemala.

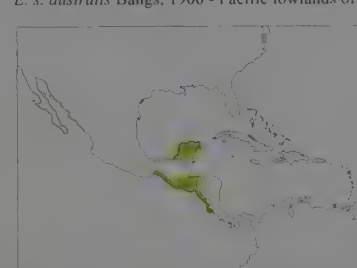
*E. s. vanrossemi* Griscom, 1929 - interior Guatemala.

*E. s. sylvestris* Carriker & Meyer de Schauensee, 1935 - Caribbean lowlands of Guatemala.

*E. s. euroaustriis* Griscom, 1929 - Caribbean lowlands of N Honduras.

*E. s. apiaster* (Lesson, 1842) - El Salvador, W Honduras and NW Nicaragua.

*E. s. australis* Bangs, 1906 - Pacific lowlands of SW Nicaragua and NW Costa Rica.



**Descriptive notes.** 33-38 cm; 44-74 g, mean 62.5 g. Tail most extremely graduated of family, central rectrices about twice as long as next pair, with bare shafts very long (c. 75 mm), flag-like racquet tip nearly twice as wide as basal part of vane, the 2 flanges decurved, dropping away from shaft on each side; bill narrow, cutting edges of both mandibles finely serrated along most of length. Both sexes nominate race conspicuous pale, slightly iridescent, turquoise-blue eyebrow, black facial mask with turquoise line below; mainly green above, with chestnut-rufous patch on mantle; flight-feathers turquoise-blue, black-tipped; tail-racquets sharply divided

into blue basal half, black distal half; throat and breast olive-green with shaggy black medial stripe edged with turquoise, belly cinnamon; bill black; legs and feet grey. Distinguished from other momotids by exceptionally long bare tail shafts, blue eyebrow, pattern of throat and breast. Juvenile duller, little or no rufous on back, little of black-and-turquoise stripe below. Races vary mainly in darkness of plumage: *bipartita* darker, greenish-olive breast and cinnamon-rufous flanks and belly sharply demarcated; *syvestris* like previous but generally darker; *euroaustriis* darker turquoise-blue eyebrow, darker wings and tail more purplish-blue; *vanrossemi* like nominate but brighter green, tawny suffusion reduced; *apiaster* with green paler, less tawny suffusion; *australis* distinctive, small and pale.

**Habitat.** Deciduous woodland and woodland edge, evergreen gallery forest, low scrubby thickets, and semi-open areas with scattered trees; also locally plantations and gardens; to 1400 m.

**Food and Feeding.** Insects, spiders, millipedes, small molluscs, earthworms, and small lizards and snakes; also fruit. Fruit in small quantities, e.g. 3-4% by volume of stomach contents in Yucatán; species recorded taken include *Stemmadenia*, *Ficus*, *Bursera*, *Ehretia* and *Gutierrezia*. Animal food seized in sudden dart to vegetation or ground, or in aerial sally; butterflies, bees, dragonflies and smaller insects also taken in flight.

**Breeding.** Lays second week May to mid-Jul (peak first half Jun) in Mexico; Apr-May in Guatemala and Honduras; may re-lay after early nest failure. Pair-bond maintained over successive years, and individuals faithful to nest-sites; either solitary or colonial, depending on availability of suitable nest-sites, some colonies of over 100 pairs. Nest typically in burrow excavated in earth bank or low cliff; burrow often curved, total length very variable, 40-244 cm, ending in enlarged nest-chamber c. 20-23 cm wide and c. 10 cm high; in Yucatán, Mexico, also uses beam-socket and ventilation holes of archaeological ruins. 2-6 eggs, most often 4, laid at intervals of c. 48 hours; incubation 18-20 days; fledging 24-31 days. In Yucatán archaeological sites, 36% of all nesting attempts failed owing to predation, probably by rat-snake (*Elaphe phascens*).

**Movements.** Returns to Yucatán breeding colonies in late Feb or Mar, a few weeks before start of nesting; extent of movement unknown, probably not great. Some seasonal movement probable also in Costa Rica, where more arid habitats occupied mainly in wet season.

**Status and Conservation.** Not globally threatened. One of the most abundant motmots, common to fairly common throughout range. Well adapted to secondary vegetation and semi-open country in areas much altered by man; also able to exploit nesting opportunities created by man, where breeding adults become conditioned to presence of human visitors.

**Bibliography.** Anon. (1998d), Binford (1989), England (2000b), Herklots (1961), Howell & Webb (1995), Klaas (1968), Land (1970), Martin, M.W. & Martin (1985), Martin, R.F. & Martin (1980), Martin, R.F. *et al.* (1989), Miller *et al.* (1957), Monroe (1968), Novaes (1992), Orejuela (1975, 1977, 1980), Owen (1861), Paynter (1955), Remsen *et al.* (1993), Scott & Martin (1983, 1986), Skutch (1947, 1983), Slud (1964), Smith, S.M. (1976, 1977), Stiles (1985), Stiles & Skutch (1989), Stotz *et al.* (1996).

## Genus *ELECTRON* Gistel, 1848

### 4. Broad-billed Motmot

#### *Electron platyrhynchum*

**French:** Motmot à bec large    **German:** Plattschnabelmotmot    **Spanish:** Momoto Picoancho  
**Other common names:** Plain-tailed Motmot ("pyrrholaemum group")

**Taxonomy.** *Momotus platyrhynchus* Leadbeater, 1829, Brazil; error = western Ecuador. Probably closely related to *E. carinatum* and, despite plumage differences, might even be conspecific; the two are similar in structure and, reportedly, in vocalizations; moreover, mixed pairing recorded in two successive seasons in Costa Rica, with apparent courtship feeding by present species; further study of taxonomic status required. Races mostly well marked; those E of Andes, lacking tail-racquets, combined as the "pyrrholaemum group", considered by some to be a separate species. Six subspecies currently recognized.

**Subspecies and Distribution.**

*E. p. minor* (Hartert, 1898) - E Honduras to E Panama.

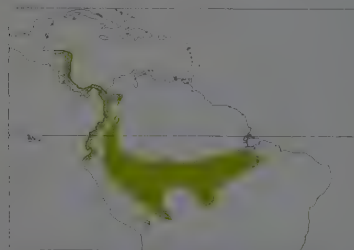
*E. p. platyrhynchum* (Leadbeater, 1829) - W of Andes from NW Colombia to SW Ecuador (El Oro).

*E. p. colombianum* Meyer de Schauensee, 1950 - lowlands N of Andes in N Colombia.

*E. p. pyrrholaemum* (Berlepsch & Stolzmann, 1902) - E of Andes from Colombia (S Meta, Caquetá) S through E Ecuador and Peru to Bolivia (Cochabamba, Santa Cruz).

*E. p. orienticola* Oberholser, 1920 - upper Amazonian Brazil (W Amazonas, Acre).

*E. p. chlorophrys* Miranda-Ribeiro, 1931 - N Brazil S of Amazon (in E Amazonas, Pará, Mato Grosso, N Goiás).



**Descriptive notes.** 31-39 cm; 56-66 g. Relative smallish motmot, appearing very large-headed in field; tail moderately graduated; bill very broad, flattened, with pronounced culmen ridge, cutting edges of both mandibles finely serrated along most of length. Both sexes nominate race rufous head, neck and breast, black mask, blue-green chin; black chest-spot(s) composed of long, broad feathers; green upperparts, bluer flight-feathers, green-blue belly; tail blue, length of bare shafts c. 24 mm, racquets tipped black; bill black, extreme tip sometimes brownish-white; legs and feet dark grey. Closely resembles *Baryphthengus*

*martii*, but smaller, black chest-spot(s) larger, throat blue-green, primaries more blue than violet. Juvenile darker, duller, with rufous below largely replaced by dark olive-green, short blue-green streak over eye, bill with whitish tip. Race *minor* paler than nominate, *colombianum* more prominent blue on throat and narrower, shorter bill; races E of Andes lack bare tail shafts and tail-racquets, *pyrrholaemum* darker rufous, much blue on throat, *orienticola* generally paler plumage than previous, *chlorophrys* distinctive with light yellowish-green superciliary markings.

**Habitat.** Humid forest and older second-growth woodland; lowlands and foothills, to 1100 m.

**Food and Feeding.** Mainly insects and their larvae, also spiders, scorpions, centipedes, small frogs and lizards; takes many large, fiercely stinging ants of genus *Panaponera*. Fruit occasionally taken, but very minor part of diet. Animal prey captured in sallies to vegetation, sometimes to ground; butterflies and dragonflies caught in flight. Regularly follows army ants, taking prey disturbed by them.

**Breeding.** Lays in Feb-May in Costa Rica; in W Colombia, stub-tailed juvenile accompanied by adults in Mar. Following details all from Costa Rica. Nest in burrow in earth bank, c. 1 m in length, 8 cm wide and 6-7 cm high at entrance. 2-3 eggs; incubation by both sexes, in very long stints, female probably longer (from about noon to following dawn), only 2 change-overs in 24 hours; total incubation period not determined; fledging 24-25 days.

**Movements.** None recorded.

**Status and Conservation.** Not globally threatened. Fairly common in some areas, but serious decline reported in W Ecuador, and other populations have undoubtedly decreased in areas suffering extensive deforestation. Brazilian population apparently rather locally distributed.

**Bibliography.** Allen (1998), Anon. (1998d), Dubs (1992), Eisenmann (1952), Hilty & Brown (1986), Kirwan & Marlow (1996), Monroe (1968), Oren & Parker (1997), Peres & Whittaker (1991), Ridgely & Gwynne (1989), Ruschi (1979), Sick (1985, 1993), da Silva *et al.* (1997), Skutch (1971, 1983), Slud (1960, 1964), Stiles & Skutch (1989), Stiles *et al.* (1999), Stotz *et al.* (1996), Watmore (1968), Willis (1980), Willis & Eisenmann (1979).

### 5. Keel-billed Motmot

#### *Electron carinatum*

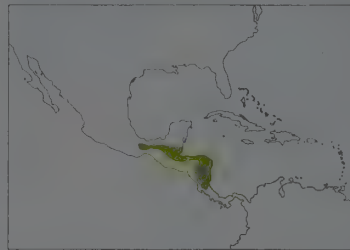
**French:** Motmot à bec caréné    **German:** Kielschnabelmotmot    **Spanish:** Momoto Carenado

**Taxonomy.** *Prionites carinatus* Du Bus de Gisignies, 1847, Guatemala.

Appears closely related to *E. platyrhynchum*, and the two might even be conspecific: they are very similar in structure and, apparently, in vocalizations, although differing notably in plumage; also,

mixed pair, with courtship feeding, recorded in two successive seasons in Costa Rica; further research required. Monotypic.

**Distribution.** S Mexico (from SE Veracruz and Oaxaca) E through Guatemala and C & S Belize to N Honduras, C & E Nicaragua and N Costa Rica.



**Descriptive notes.** 30.5-38 cm; male 65 g. Smallish motmot with moderately graduated tail, central rectrices with racquets; bill very broad, and flattened, with a pronounced culmen ridge, and cutting edges of mandibles finely serrated for most of length. Both sexes have sharply demarcated rufous forehead, black mask through eye with turquoise-blue streak above; rest of upperparts green; underparts greenish to greenish-cinnamon with pale turquoise chin, black chest-spot(s); bill black, with tip horn-coloured. Juvenile apparently undescribed.

**Habitat.** Inhabits humid evergreen forest, especially in areas with steep-sided gulleys and streams. In Costa Rica, occurs only in forests of foothills and neighbouring lowlands. Generally occurs below 760 m, but recorded up to 1555 m in Honduras.

**Food and Feeding.** No details of diet; apparently similar to that of *E. platyrhynchum*. Forages by aerial sallies from perch.

**Breeding.** No details recorded. Males proclaim territories noisily in period Jan-Mar. In one area in Belize, steep-sided unexcavated Mayan structures used as nest-burrow sites; in another area, apparently steep banks along seasonal streams.

**Movements.** None recorded.

**Status and Conservation.** VULNERABLE. Overall range fairly extensive, but heavily fragmented and lying within area where habitat intensely threatened. Until recently, known from only a small number of widely scattered localities; in Mexico was thought to be extinct as a result of habitat loss, with no records since 1952, but rediscovered in Oaxaca in 1995. Considered rare elsewhere in range. Recent research suggests that Belize may have largest populations, though many of these are small, and isolated by forest clearance; at one locality 16-20 birds estimated in area of 2000 ha, in another 20-25 birds in area of 6477 ha. Most Belize populations now within protected areas, but long-term survival still uncertain; some males in small territories observed to be unable to attract mates. Elsewhere, habitat destruction has been proceeding rapidly, especially in Mexico; forest clearance is mainly to prepare for settlement and for conversion to agriculture, especially plantations of bananas

**Bibliography.** Ah (1994), Anon. (1998d), Collar & Andrew (1988), Collar, Gonzaga *et al.* (1992), Collar, Wege & Long (1997), Fogden (1993), Hernández-Baños *et al.* (1995), Howell & Webb (1992, 1995), Land (1970), Lowery & Dalquest (1951), Miller, A.H. *et al.* (1957), Miller, B.W. & Miller (1996), Miller, C.M. (1995), Miller, C.M. & Jug (1991), Monroe (1968), Parker *et al.* (1994), Pearman (1994), Slud (1964), Stattersfield & Capper (2000), Stiles (1985), Stiles & Skutch (1989), Stotz *et al.* (1996), Wege & Long (1995).

## Genus *BARYPTHENGUS*

Cabanis & Heine, 1859

### 6. Rufous Motmot

#### *Baryphthengus martii*

**French:** Motmot roux    **German:** Zimtbrustmotmot    **Spanish:** Momoto Yeruvá Occidental

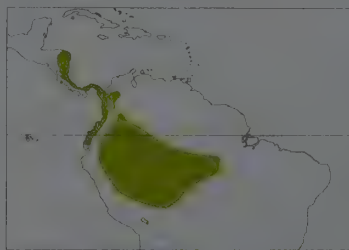
**Taxonomy.** *Prionites martii* Spix, 1824, Pará, Brazil.

May form a superspecies with *B. ruficapillus*. Structurally similar and has often been regarded as conspecific, but differences in both voice and plumage now generally considered sufficient to warrant treatment as separate species. Populations of Nicaragua and Costa Rica formerly separated as race *costaricensis*, on grounds of larger size and fairly minor differences in coloration, but subsequently found to overlap in both aspects with birds from Panama and Colombia, so this form now considered inseparable from *semirufus*. Two subspecies recognized.

**Subspecies and Distribution.**

*B. m. semirufus* (P. L. Sclater, 1853) - E Honduras, E Nicaragua, Caribbean slopes of Costa Rica and Panama, NW Colombia and W Ecuador W of Andes.

*B. m. martii* (Spix, 1824) - Amazonian Basin in E Ecuador, SE Colombia and NW Brazil (E to R Tapajós) S to E Peru and N Bolivia.



**Descriptive notes.** 42-47 cm; male 146-160 g (*martii*), 185-193 g (*semirufus*); female 153-173 g (*martii*), 170-208 g (*semirufus*). Very large motmot with long and narrow tail very markedly graduated, central rectrices c. 110 mm longer than next pair, but nominate without racquets; bill decurved, rather narrow, cutting edges of both mandibles very coarsely serrated along middle part. Both sexes of nominate race have rufous head, neck and breast, black eye-mask and chest-spot(s); upperparts green, primaries violet-blue; belly bluish-green; bill black; legs and feet dark grey. Darker variant shows more saturated coloration, and also darker eyes. Differs from strikingly similar *Electron platyrhynchum* in larger size, plain throat, colour of primaries, smaller chest-spot(s). Juvenile paler, duller, no black chest-spot. Race *semirufus* larger than nominate, belly bluer, central rectrices with bare distal shafts and medium-sized terminal racquets.

**Habitat.** Humid forest, older second-growth woodland, occasionally semi-open areas with tall trees; to 1400 m.

**Food and Feeding.** Very versatile feeder: consumes great variety of invertebrates and small vertebrates, also many fruits. Invertebrates include insects and insect larvae, spiders, millipedes, small crustaceans. Among vertebrates are lizards, frogs (including poisonous frog *Dendrobates auratus*),



and small fish. Fruits recorded in diet include those of nutmegs (*Virola*), palms, and *Heliconia*. Analysis of stomach contents showed nearly one-third containing fruit only, slightly lesser proportion with both fruit and arthropods. Animals taken mainly from lower vegetation or ground, occasionally from water; fruits plucked in flight. Regularly accompanies mixed-species flocks following army ants.

**Breeding.** Lays in Mar-Jun in Costa Rica; in Panama, young being fed in late Jun and occupied nests in Feb-Sept. Nest a long winding burrow, 4-5 m long, in streamside bank or side of pit or mammal den. Clutch size and incubation and fledging periods not recorded.

**Movements.** None recorded.

**Status and Conservation.** Not globally threatened. Fairly common in most of range; common in some areas, e.g. Costa Rica. Tolerance of secondary woodland and even semi-open habitats provides it with some immunity to clearance of primary forest.

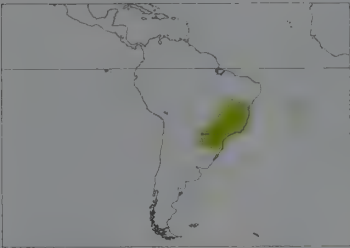
**Bibliography.** Allen (1998), Anon. (1998d), Best *et al.* (1997), Eisenmann (1952), Hilty & Brown (1986), Kirwan & Marlow (1996), Master (1998, 1999), Oren & Parker (1997), Peres & Whittaker (1991), Ridgely & Gwynne (1989), Ruschi (1979), Salaman *et al.* (1999), Sick (1985, 1993), da Silva *et al.* (1997), Skutch (1971, 1983), Slud (1960, 1964), Stiles & Skutch (1989), Stiles *et al.* (1999), Stotz *et al.* (1996), Taylor (1995), Traylor (1958), Wetmore (1968), Willis (1980), Willis & Eisenmann (1979).

7. Rufous-capped Motmot  
*Baryphthengus ruficapillus*

**French:** Motmot oranroux      **German:** Rotkopfmotmot      **Spanish:** Momoto Yeruvá Oriental

**Taxonomy.** *Baryphonus ruficapillus* Vieillot, 1818, Lima, Peru; error = south-east Brazil. May form a superspecies with *B. martii*, and often regarded as conspecific. Despite structural similarities, however, considerable plumage differences and reported difference in voice now generally considered sufficient to warrant treatment as separate species. Proposed Brazilian races *aeruginosus* (Minas Gerais, Rio de Janeiro), *septentrionalis* (São Paulo) and *abreui* (Paraná) shown in recent study all to be based on individual variation, without geographical significance; *berlai* (Goiás) regarded as an invalid name. Monotypic.

**Distribution.** E & S Brazil (Bahia and C Goiás S to N Rio Grande do Sul), E Paraguay and NE Argentina (Misiones).



**Descriptive notes.** 42 cm; 140-151g. Large motmot. Both sexes have rufous crown and nape, and black eye-mask bordered with turquoise; green upperparts, including wing-coverts and tail; primaries bright blue-green; throat and breast olive-green, black chest-spot(s), rufous restricted to band across belly, lower belly bluish-green; iris amber or ruby-brown; bill black; legs and feet dark grey. Differs from *B. martii* in generally greener and duller plumage, with less rufous, tail shorter and markedly less graduated, central rectrices narrowing to blunt end without racquets. Juvenile duller than adult.

**Habitat.** Primary lowland forest, and gallery forest along watercourses; to 1200 m.

**Food and Feeding.** Mainly large insects and insect larvae, land molluscs, small reptiles, small mammals and small birds; also some fruit. Occasionally follows army ants, taking prey disturbed by them.

**Breeding.** Excavation of burrows recorded in Jan-Apr (when earth damp from summer rain); lays probably in Sept-Oct, with records of nestlings being fed in second half of Nov and recently fledged young early Dec. Nest a burrow in earth bank, more than 1 m in length; 2 occupied burrows recorded 23 cm apart. 2-3 eggs. No further details.

**Movements.** None recorded.

**Status and Conservation.** Not globally threatened. No information on numbers, but apparently not uncommon locally. Has, however, undergone widespread decline as result of deforestation. Occurs in several protected areas, e.g. Iguazú National Park and Urugua-i Provincial Park, Argentina, being frequently recorded in both of these.

**Bibliography.** Aleixo & Galetti (1997), dos Anjos & Schuchmann (1997), dos Anjos *et al.* (1997), Belton (1984), Canevari *et al.* (1991), Capper *et al.* (2000), Chebez *et al.* (1999), Goerck (1999), Guix (1995), Hayes (1995), Lowen *et al.* (1995), Madroño *et al.* (1997), Mitchell (1957), Parker & Goerck (1997), de la Peña (1994), Pereyra (1950), Ruschi (1979), Saibene *et al.* (1996), Schubart *et al.* (1965), Sick (1985, 1993), da Silva *et al.* (1997), Silveira (1998), Stotz *et al.* (1996), Straube & Bornschein (1991), Willis & Oniki (1991).





# Genus *MOMOTUS* Brisson, 1760

## 8. Russet-crowned Motmot

### *Momotus mexicanus*

**French:** Motmot à tête rouse **German:** Braunscheitelmotmot **Spanish:** Momoto Mexicano

**Taxonomy.** *Momotus Mexicanus* Swainson, 1827, Temiscáltepec, Mexico. Geographical variation in main part of range rather moderate, and probably clinal, with palest populations occurring in northernmost areas; isolated S population *castaneiceps* more distinctive, and has been proposed as possibly representing a distinct species. Four subspecies currently recognized.

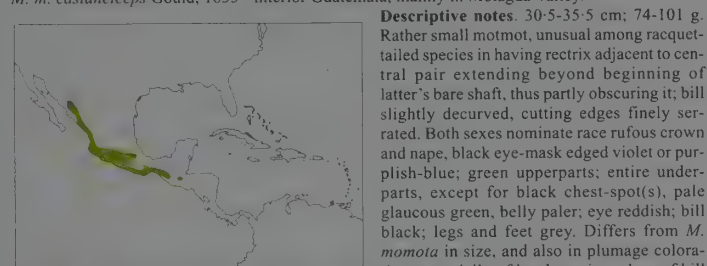
#### Subspecies and Distribution.

*M. m. vanrossemi* R. T. Moore, 1932 - NW Mexico in S Sonora and northernmost Sinaloa, and adjacent SW Chihuahua.

*M. m. mexicanus* Swainson, 1827 - Sinaloa and Durango S to Guerrero, W Oaxaca and extreme W Veracruz.

*M. m. saturatus* Nelson, 1897 - E Oaxaca and Chiapas, and adjacent SW Guatemala.

*M. m. castaneiceps* Gould, 1855 - interior Guatemala, mainly in Motagua Valley.



**Descriptive notes.** 30-5-35-5 cm; 74-101 g. Rather small motmot, unusual among racquet-tailed species in having rectrix adjacent to central pair extending beyond beginning of latter's bare shaft, thus partly obscuring it; bill slightly decurved, cutting edges finely serrated. Both sexes nominate race rufous crown and nape, black eye-mask edged violet or purplish-blue; green upperparts; entire underparts, except for black chest-spot(s), pale glaucous green, belly paler; eye reddish; bill black; legs and feet grey. Differs from *M. momota* in size, and also in plumage coloration, especially of head; cutting edges of bill

somewhat more finely serrated. Juvenile duller, eyes brown. Race *vanrossemi* generally paler plumage than nominate; *saturatus* larger, generally darker; *castaneiceps* markedly larger, crown to hindneck darker, bright chestnut, anterior part of black headband margined beneath by greenish-white instead of blue.

**Habitat.** Arid to semi-arid woodland and woodland edge, and semi-open areas with trees and hedges; to 1800 m.

**Food and Feeding.** Mainly large insects, taken from ground, foliage or air; also small snakes. Fruit apparently not recorded.

**Breeding.** Lays in Apr-May. Nest in burrow excavated in earth bank or roadside cutting. 3 eggs; incubation and fledging periods not documented.

**Movements.** None recorded.

**Status and Conservation.** Not globally threatened. Considered to be common to fairly common throughout range. Evident tolerance of, and probable adaptation to, arid and semi-arid habitats that have been modified by man should ensure this species' survival in foreseeable future. Poorly known; research required on ecology and biology.

**Bibliography.** Anon. (1998d), Binford (1989), Blake & Hanson (1942), Dearborn (1907), Howell & Webb (1995), Land (1970), Miller *et al.* (1957), Prinsen & Kok (1999), Rowley (1966, 1984), Schaldach (1963), Stotz *et al.* (1996).

## 9. Blue-crowned Motmot

### *Momotus momota*

**French:** Motmot houtouc **German:** Blauscheitelmotmot **Spanish:** Momoto Común  
**Other common names:** Lesson's Motmot ("*lessonii* group"); Caribbean/Tawny-bellied Motmot ("*subrufescens* group"); Blue-diademed Motmot ("*momota* group")

**Taxonomy.** *Ramphastos momota* Linnaeus, 1766, Cayenne.

Quite closely related to *M. aequatorialis*, and sometimes treated as conspecific, but significant differences in size and plumage, as well as ecological differences, almost certainly justify their being ranked as separate full species. Very wide distribution and considerable geographical, as well as individual, variation have led to numerous races being named; situation complex, however, and taxonomic revision needed. Races *goldmani*, *exiguus* and *lessonii* sometimes referred to as "*lessonii* group", *conexus*, *subrufescens*, *spatha* and *osgoodi* as "*subrufescens* group", and all other populations E & S from NC Colombia as "*momota* group"; these groups, along with *coeruliceps*, sometimes thought possibly to represent four separate species; in particular, populations in E Panama differ from those in W in several plumage characters, as well as in size and, apparently, voice, with no recorded intergradation, suggesting they are possibly distinct species; also, isolated Trinidad and Tobago race *bahamensis* rather distinct, would probably be considered separate species on basis of molecular genetics. Populations of E Panama and NW Colombia, described as race *reconditus*, now included in *conexus*. Twenty subspecies currently recognized.

#### Subspecies and Distribution.

*M. m. coeruliceps* (Gould, 1836) - NE Mexico (E Nuevo Leon, S Tamaulipas).

*M. m. goldmani* Nelson, 1900 - E Mexico (Veracruz, N Oaxaca, Tabasco) and neighbouring Guatemala (Petén).

*M. m. exiguus* Ridgway, 1912 - Yucatán Peninsula.

*M. m. lessonii* Lesson, 1842 - S Mexico (Chiapas) E to W Panama.

*M. m. conexus* Thayer & Bangs, 1906 - C Panama to NW Colombia.

*M. m. subrufescens* P. L. Sclater, 1853 - Caribbean coast of N Colombia (S to Magdalena Valley) to Venezuela.

*M. m. spathula* Wetmore, 1946 - Guajira Peninsula (Serranía de Macuira), in N Colombia.

*M. m. osgoodi* Cory, 1913 - NW Venezuela and adjacent Colombia (to Norte de Santander).

*M. m. bahamensis* (Swainson, 1838) - Trinidad and Tobago.

*M. m. olivaresi* Hernández & Romero, 1978 - NC Colombia (Santander, Boyacá).

*M. m. argenticinctus* Sharpe, 1892 - W Ecuador and NW Peru W of Andes.

*M. m. microstephanus* P. L. Sclater, 1858 - lowlands E of Andes in E Colombia, W Venezuela, E Ecuador, NE Peru and NW Brazil (E to upper R Negro).

*M. m. momota* (Linnaeus, 1766) - from R Orinoco E to N Brazil (Amapá), S to N bank of lower Amazon.

*M. m. ignobilis* Berlepsch, 1889 - E Peru, N Bolivia, and probably W Brazil.

*M. m. simplex* Chapman, 1923 - N Brazil S of Amazon (from near Peru border E to upper R Xingú, S to N Mato Grosso and C Goiás).

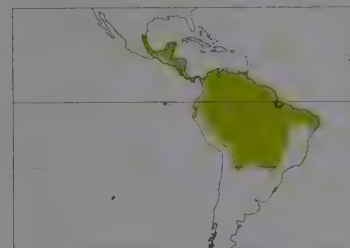
*M. m. cametensis* Sneath, 1912 - lower R Xingú (probably from lower R Tapajós) E to R Tocantins.

*M. m. parensis* Sharpe, 1892 - from Amazon mouth E to Piau and probably W Alagoas.

*M. m. marcgraviana* Pinto & Camargo, 1961 - Paraiba, in NE Brazil.

*M. m. nattereri* P. L. Sclater, 1858 - N & C Bolivia (mainly along Andean foothills).

*M. m. pilcomajensis* Reichenow, 1919 - E Bolivia and N Argentina E to S Brazil (to S Goiás, S São Paulo and NW Paraná).



**Descriptive notes.** 38-43 cm; 77-102 g (*exiguus*), 97-148 g (*lessonii*), 99-114 g (*bahamensis*), 120-160 g (*momota*), 105-141 g (*ignobilis*), 133-145 g (*parensis*), 85-118 g (*pilcomajensis*). Mid-sized to large motmot with blue on crown, tail long and racquet-tipped; bill slightly decurved, both mandibles with coarse serrations along most of length of cutting edges. Both sexes nominate race black crown bordered by turquoise and violet; black mask through eye extending through auriculars to sharp tip, and partly bordered above and below with turquoise; rufous hindneck, green back; greenish underparts more or less suffused

with cinnamon; 1 or 2 black chest-spot(s) bordered turquoise, number of spots visible depending on whether plumage is neat or dishevelled; eye red; bill black; legs and feet grey. Juvenile like adult, but entire crown suffused with greenish-blue, black mask smaller and more sooty, no black chest-spot. Races vary in size, largest in tropical lowlands E of Andes, smaller in peripheral parts of range, and in plumage, upperparts varying from dark green to tawny-washed, foreneck and chest from light olive-green to tawny rufous with same tint paler on posterior underparts, but variation highly complex: e.g. *lessonii* mostly light olive-green underparts, *exiguus* similar but smaller, *goldmani* paler, *coeruliceps* crown all blue with forehead greenish; *conexus* mostly dull tawny, washed olive on breast; *pilcomajensis* dark green above, tawny-rufous belly; *bahamensis* distinctive, small, mainly rufous below.

**Habitat.** Humid forest, seasonal forest, semi-arid open woodland, clearings with scattered trees, plantations, and locally gardens; in Tobago also in more exposed situations, cocoa plantations, even sandy beaches and pasture land with large trees. To 1600 m in Mexico and Guatemala, 2150 m in S Costa Rica, 1300 m in Colombia.

**Food and Feeding.** Insects and many other invertebrates, including snails, centipedes and earthworms; also small reptiles and mammals, occasionally small birds and nestlings; also regularly fruit. Semi-tame birds in Tobago accept soaked bread, cheese and other human offerings. Fruits include arillate fruit of nutmeg *Compsonura sprucei* (Myristicaceae), *Eugenia jambos* (Myrtaceae), *Ficus* and *Castilla elastica* (Moraceae), *Simarouba glauca* (Simaroubaceae) and *Sloanea trinitensis* (Tiliaceae). Of 39 faecal samples from SC Brazil (Mato Grosso do Sul), 46% contained only arthropods, 41% arthropods and fruits, and 13% only fruits. Prey taken in sallies to vegetation, also regularly from ground, where bill used to probe into soft earth or brush away leaf litter. Fruits plucked in aerial sallies. Often follows army ants, taking invertebrates disturbed by them.

**Breeding.** Lays in May-Jun in S Mexico, Mar-May in Costa Rica, Apr-May in Trinidad, Mar-Jul in Tobago, Sept-Oct and Jan-Feb in French Guiana, and Sept-Dec in S Brazil, N Argentina and Bolivia; post-breeding moult Jan-Jun in SC Brazil (Mato Grosso do Sul). Nest-burrow excavated usually in earth bank, very variable in length, from 60 cm to c. 4 m, not always straight, entrance often well concealed; also in side of pit or hollow in ground, locally in archaeological ruins. 3-5 eggs in Yucatán, 3-4 in Costa Rica, 3 in Trinidad and Tobago, few records from elsewhere; incubation c. 21 days; fledging 29-32 days, once 38 days (Costa Rica).

**Movements.** None recorded.

**Status and Conservation.** Not globally threatened. Common to fairly common in Mexico; common in much of Costa Rican range, and reasonably common in rest of Central and South American parts of its distribution. Much commoner in Tobago, where familiar with man and locally a tourist attraction, than in neighbouring Trinidad. Very wide range and tolerance of man-altered habitats should ensure its survival. Occurs in numerous protected areas.

**Bibliography.** Anon. (1998d), Binford (1989), Canavari *et al.* (1991), Chebez (1994), Cohn-Haft *et al.* (1997), Ericson & Amarilla (1997), Feldman (1988), French (1991), Fjeldså & Krabbe (1990), Friedmann (1948), Guix (1995), Haverschmidt & Mees (1994), Hayes (1995), Hayes *et al.* (1990), Hernández & Romero (1978), Hernández-Baños *et al.* (1995), Hilty & Brown (1986), Howell & Webb (1995), Klaas (1968), Larcombe (1991), Lindholm (1991), Lowery & Dalquest (1951), Melo & Piratelli (1999), Meyer de Schauensee & Phelps (1978), Monroe (1968), Orejuela (1975, 1977, 1980), Paynter (1955, 1957), de la Peña (1994), Pinto & Camargo (1961), Ridgely & Gwynne (1989), Robinson (1997), Ruschi (1979), Rutgers & Norris (1977), Schubart *et al.* (1965), Short (1975), Siek (1985, 1993), Skutch (1964, 1983), Slud (1964), Snyder (1966), Stiles & Skutch (1989), Stotz *et al.* (1996), Straube & Bornschein (1995), Tostain *et al.* (1992), Traylor (1958), Wetmore (1968).

## 10. Highland Motmot

### *Momotus aequatorialis*

**French:** Motmot d'Équateur **German:** Hochlandmotmot **Spanish:** Momoto Serrano  
**Other common names:** Equatorial Motmot

**Taxonomy.** *Momotus aequatorialis* Gould, 1858, Archidona, Ecuador.

Fairly closely related to *M. momota*, and sometimes treated as a well-marked highland race thereof, but notable differences in size and plumage, as well as in ecology, probably justify its separation as a full species. Two subspecies recognized.

#### Subspecies and Distribution.

*M. a. aequatorialis* Gould, 1858 - subtropical and lower temperate zones of Andes in W Colombia, and E slopes of Andes in Ecuador.

*M. a. chlorolaemus* Berlepsch & Stolzmann, 1902 - subtropical Andes in E Peru; possibly also S to N Bolivia.

**Descriptive notes.** 48 cm; 123-176 g. Large motmot with tail long and racquet-tipped; bill slightly decurved, with coarse serrations along most of length of cutting edges. Both sexes nominate race black crown encircled by turquoise on forehead, this becoming dark blue on hindcrown; black



mask with turquoise line below, turquoise streak drooping across black auriculars and separating sharp tip from rest of mask; grass-green above and olive-green below, with variable brownish suffusion, black chest-spot(s); eye red; bill black; legs and feet grey. Differs from *M. momota* in somewhat larger size, lighter green coloration, and details of head pattern. Juvenile generally duller, lacking black chest-spot. Race *chlorolaemus* rather similar to nominate, but little or no tawny suffusion on green underparts, throat more bluish, less green.

**Habitat.** Occupies subtropical and lower temperate montane forest, normally at elevations of 1500-2400 m, but rarely occurring up to 3100 m.

**Food and Feeding.** Remains of beetles, other large insects, and caterpillars have been recorded on specimen labels. No other details available.

**Breeding.** Gonadal condition of specimens indicates probable laying in second half of Mar and in Sept; eggs collected in Colombia, but without precise data. No further information available.

**Movements.** None recorded.

**Status and Conservation.** Not globally threatened. Seems to be generally common in suitable habitats, but no information on numbers. Uncertainty regarding taxonomic status has hampered preparation of clear picture of status. Very few precise data available; further research required. Distribution is probably continuous down E slope of Andes in S Colombia and N Peru, but no actual records; this species may also be present in premontane zone of N Bolivia (La Paz); surveys needed in order to establish precise limits of distribution. Occurs in several protected areas, e.g. Podocarpus National Park, Ecuador.

**Bibliography.** Balchín & Toyne (1998), Best *et al.* (1997), Fjeldså & Krabbe (1990), Hilty & Brown (1986), Lletget (1942), Miller (1963), Parker *et al.* (1982), Sagot (1998), Stotz *et al.* (1996), Taylor (1995).





Class AVES  
Order CORACIIFORMES  
Suborder MEROPEs  
**Family MEROPIDAE (BEE-EATERS)**



- Medium-sized, brightly coloured birds, with long, decurved bill, medium to long wings, short legs and many with tail-streamers.
- 16-35 cm.



- Old World.
- Open areas, forest edge and clearings, in warm climates.
- 3 genera, 25 species, 52 taxa.
- No species threatened; none extinct since 1600.

### Systematics

There is a broad measure of agreement that the living families most closely related to the bee-eaters are the kingfishers (Alcedinidae), the motmots (Momotidae) and the todies (Todidae). That conclusion has been reached on the basis of detailed anatomical work, mainly in the heyday of comparative zoology a century ago, and is supported by modern studies. The four families share a peculiar structure of the middle-ear bones, and they have the same types of jaw apparatus and leg musculature. More recently, analytical studies of DNA-DNA hybridization have shown considerable similarities at the molecular level. Almost as persuasive are the obvious, if superficial, external similarities: all have bright plumage with shiny greens and blues predominating, they are large-headed and short-necked, and they have very short legs and weak feet, with two toes joined together at their proximal bones. In addition, the members of these families are chiefly tropical, insect-eating, hole-nesting birds; they may differ strikingly in the ways they feed, but they exhibit equally telling similarities in breeding biology.

The trogons (Trogonidae) also share most of these characters. Indeed, many taxonomists believe that the five families, comprising the bee-eaters, kingfishers, motmots, todies and trogons, form an ancient natural assemblage best segregated at subordinal or even ordinal level.

The bee-eaters have often been classified in the same order as the rollers (Coraciidae), the hoopoes (Upupidae) and the wood-hoopoes (Phoeniculidae), and they may also be distantly related to the puffbirds (Bucconidae) and the jacamars (Galbulidae). In the last case, however, any "relationship" would appear to be tenuous in the extreme. The fossil evidence is that bee-eater-like, kingfisher-like and roller-like birds all existed forty million or more years ago, in France, and that some other divisions between the living families of coraciiform birds may be deeper still. There are other fossil bee-eaters, from deposits in Austria, Israel and Russia, but they are recent, have been attributed to the European Bee-eater (*Merops apiaster*), and tell us nothing about the family's evolutionary history.

Opinion is divided as to whether the family is most closely related to the kingfishers, to the motmots and todies, or to the rollers or trogons. In a monograph of bee-eaters published in 1984, C. H. Fry cited several specialists who supported one or another of the first three candidates. Nowadays, the trogons seem to be out of the running. A personal evaluation is that the king-

fisher family is the bee-eaters' sister-group, even if at a remove of tens of millions of years from their common ancestor. The Momotidae and the Todidae are New World families, while the bee-eaters and nearly all kingfisher species belong to the Old World. Finally, there may just be a phylogenetic basis for the quite unexpected discoveries in recent years that bee-eaters occasionally dive into water to catch fish, and that kingfishers sometimes hawk successfully for bees and other airborne insects.

There are 25 species of bee-eater, mostly African, with a few in southern Asia and South-east Asia, two quite far north in Eurasia and one in Australia. Relationships among them have not been worked out by the principles of numerical taxonomy, nor revealed



*The Carmine Bee-eater has two widely separated populations, which differ in throat colour, and, to a minor degree, in tail length and weight. This combination of factors has led many to regard the two as separate species. However, since their voice, ecology, and breeding and migrating behaviour are virtually identical, it may be more appropriate to consider them merely different subspecies. How they might interact in a hypothetical area of overlap remains a matter for speculation.*

[*Merops nubicus nubicoides*, Okavango Delta, Botswana.  
Photo: Adrian Bailey/  
Oxford Scientific Films]

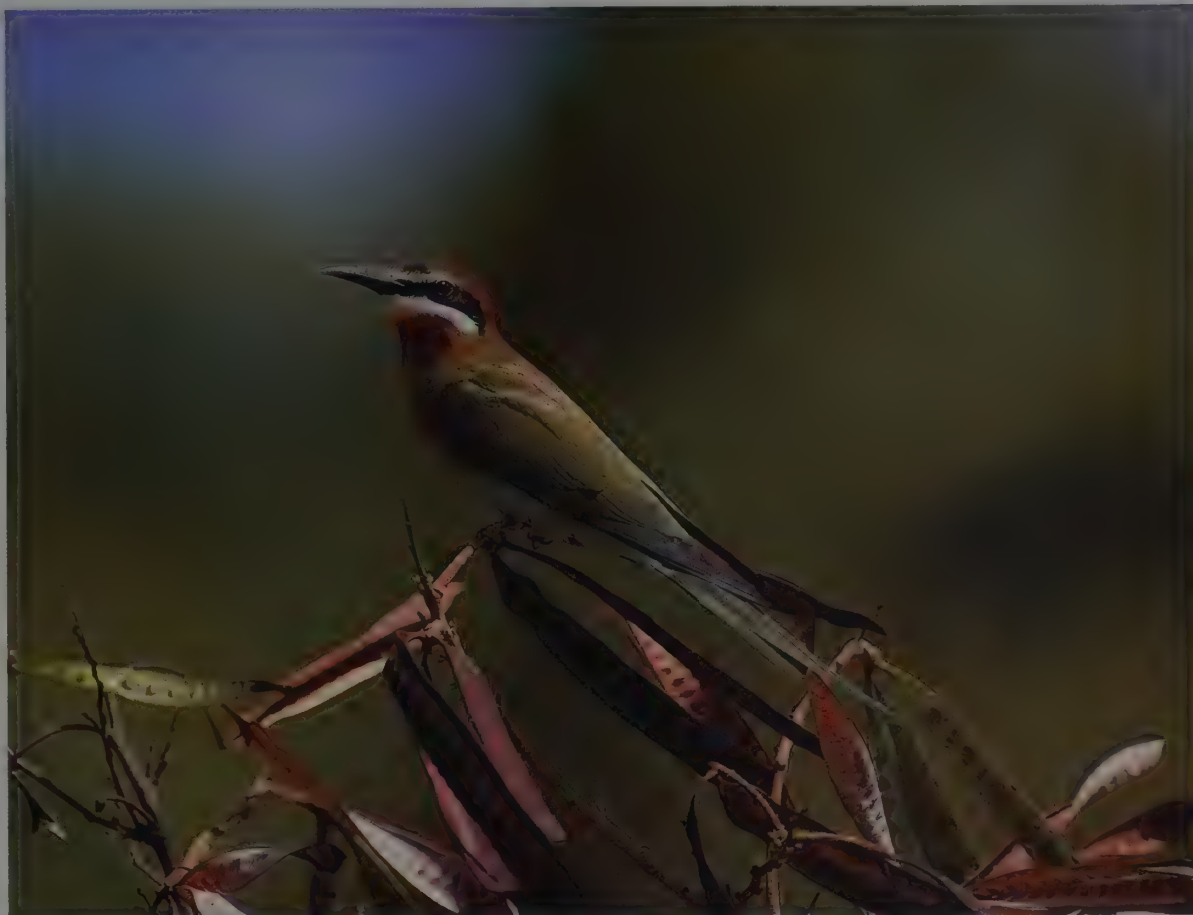


The Olive Bee-eater is one of a trio of closely related forms along with the Blue-tailed (*Merops philippinus*) and Blue-cheeked Bee-eaters (*Merops persicus*).

These three have sometimes been lumped as a single species. An alternative line is to recognize two species, and over the years all three possible combinations for converting these three forms into two species have been proposed. Given the uncertainty surrounding the relationships of the three, together with fairly notable differences in plumage, the most appropriate course is probably to recognize three species forming a superspecies.

[*Merops superciliosus superciliosus*,

Mayotte (Maore), Comoros. Photo: Roland Seitre/Bios]



by biochemical research. Nevertheless, appraisals of plumage colours and patterns, vocal similarities and differences, tail shape and other characters, in relation to quite detailed knowledge of breeding ranges, do enable the mutual affinities of several species to be inferred with some confidence.

Although the bee-eater species vary in flight characteristics, wingtip shape and tail form, and differ quite dramatically in coloration, territoriality, breeding coloniality and the degree of co-operative breeding or helping at the nest, the family is morphologically uniform. Three genera are recognized. These are *Nyctyornis* and *Meropogon* of South-east Asian forest, with three species between them, and *Merops*, which contains 22 species.

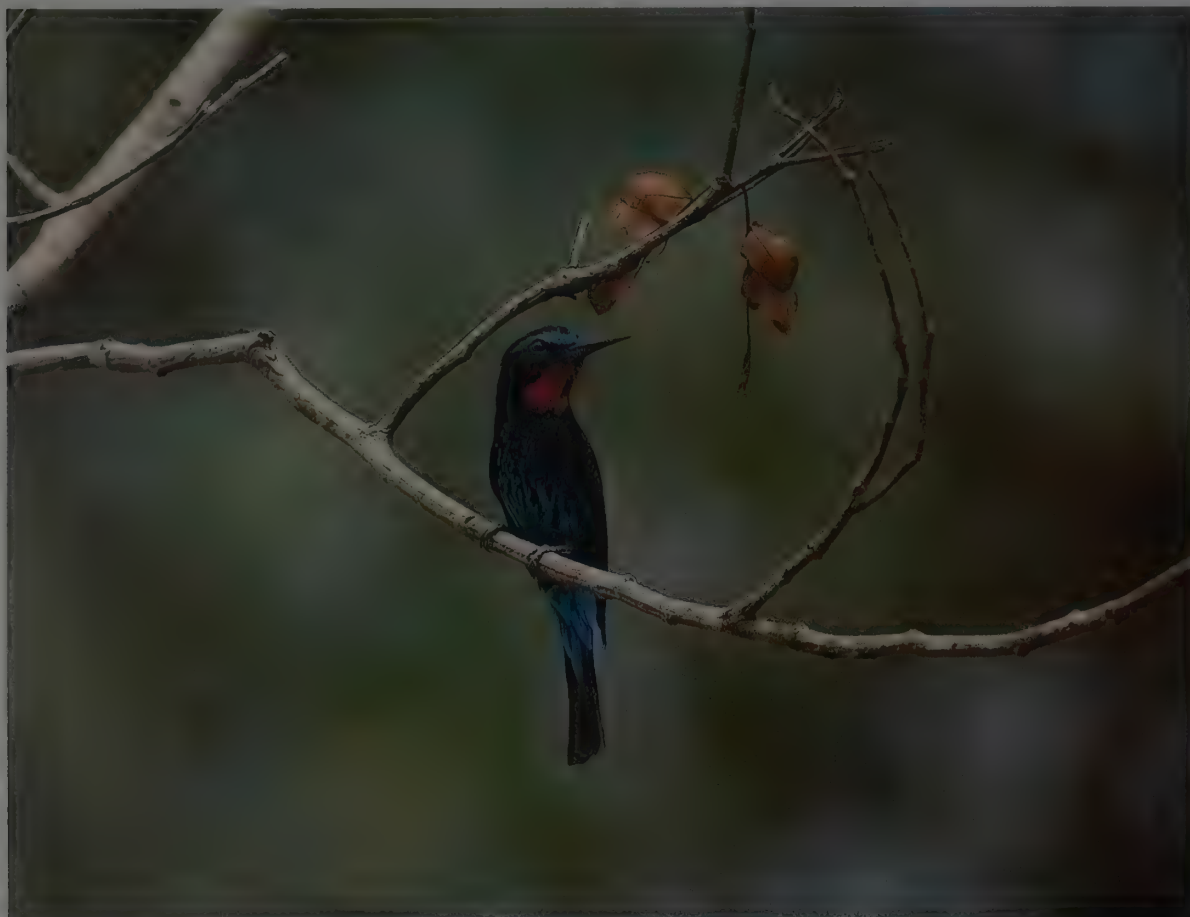
Both the Blue-bearded Bee-eater (*Nyctyornis athertoni*) and the Red-bearded Bee-eater (*Nyctyornis amictus*) have full, mainly green plumage with long, loose throat feathers, round-ended wings with seventh and eighth primaries the longest, and a long, square-ended tail which is mainly yellow below. The bill is robust, with the culmen arched, ridged and grooved and the nostrils screened by feathers. The birds perch for long periods half-hidden by leaves at middle levels in hill forest, in places from where they can scan across a treefall clearing, roadway, or treetops farther downhill. From time to time they fly out a few metres, without the élan with which smaller bee-eaters pursue fast-flying insects, to hawk a large carpenter-bee (*Xylocopa*), a hornet or a cicada. *Nyctyornis* bee-eaters are large, weighing over 80 g; although they can give quite spirited chase to flying ants or termites, they are relatively sluggish, quite lacking the grace in deportment and flight that so strongly characterizes other bee-eaters. Their voices are qualitatively quite different from those of *Merops* species, and are, if anything, roller-like. So also, incidentally, is their pterylosis, as was shown by F. E. Bedard in H. E. Dresser's 1884-1886 monograph of the Meropidae, while the bee-eaters and the true coraciid rollers also share a genus of feather lice. Overall, the Blue-bearded and Red-bearded Bee-eaters, still not known well, seem to be less specialized in their

diets and hunting behaviour than are the bee-eaters of the genus *Merops*.

The Purple-bearded Bee-eater (*Meropogon forsteni*), endemic to Sulawesi, has some *Nyctyornis*-like features. These are rather short, round-ended wings, and long throat feathers which, with shorter ones on the sides of the neck, can be erected to form a ruff. Other characters are like those of *Merops*: a slender bill with the culmen neither ridged nor grooved and the nostrils not screened by feathers, elongated central tail feathers, and a lively disposition. This species, too, is a rainforest bird, but it lives rather more out in the open, hunting from dead, emergent treetop branches at the edge of the forest. In some ways it bears a striking resemblance to West Africa's Black-headed Bee-eater (*Merops breweri*), and the two have almost exactly the same tail shape, colour and pattern. *Meropogon*, however, possesses one pair of ribs more than does *Merops*, or at least one more than *Merops apiaster*, and is probably only a distant relative.

Many authors have allocated the remaining 22 species to several genera, in some cases as many as six. The characters employed to diagnose those six, such as the length of the central pair of tail feathers and the shape of the outermost primary, have not, however, proved to be very helpful in revealing phylogenetic relationships. In a review in 1969, C. H. Fry returned all 22 species to *Merops*, identifying some clusters of related species, and since then regional authorities have broadly accepted that arrangement. This is not to say that the last word has been given, and we do not yet know whether the structure of mitochondrial cytochrome-*b* DNA, for instance, might suggest a different phylogenetic picture and systematic arrangement.

Three species of *Merops* live sympatrically in and around lowland West African and Congo Basin forests. These are the Blue-headed Bee-eater (*Merops muelleri*) and Black Bee-eater (*Merops gularis*), and the large Black-headed Bee-eater. Both of the first two have a scarlet throat, with otherwise dark plumage lacking any green. Of the two subspecies of Blue-headed, the one living west of the Sanaga River system in south Cameroon



Over the years the generic position of the Black Bee-eater has been debated by various authors. When originally named way back in 1798, it was placed in Linnaeus's genus *Merops*. Thereafter, it was at times separated in the genus *Meropiscus*, along with the Blue-headed Bee-eater (*Merops muelleri*). An alternative proposal involved the grouping of these two species with five other small, round-winged, streamerless bee-eaters in the genus *Mellitophagus*, and this treatment was in vogue for quite some time. However, in more recent times the vast majority of authors have abandoned this genus, lumping all seven species back into a rather broad-based *Merops*.

[*Merops gularis gularis*, Tai Forest National Park, Ivory Coast.  
Photo: A. Greensmith/Ardea]

has elongated central tail feathers, whereas the other does not. The subspecies of the Black Bee-eater, one with a blue eyestripe and small red throat patch, the other with no eyestripe and a large red patch, meet at the Nigeria-Cameroon border. Something of an anomaly with its resemblance to the Purple-bearded Bee-eater of Sulawesi, the Black-headed Bee-eater has little in common with the other two.

Four small or medium-sized bee-eaters living in African grassland and woodland, more or less sympatrically although in distinctively different habitats, are closely related to each other. They are the Little (*Merops pusillus*), Blue-breasted (*Merops variegatus*), Cinnamon-chested (*Merops oreobates*) and Swallow-tailed Bee-eaters (*Merops hirundineus*). Characters which they share are voice, wing shape, green upperparts, a yellow throat, a black or purple pectoral band or gorget, mainly rufous remiges which are black-tipped, and a tail which is green and rufous, dusky-ended, whitish-tipped, and with the outer feathers hooked or elongated; all four also have a juvenile plumage that is dappled below and lacks the pectoral band. One uncertainty is whether the highland Ethiopian form *lafresnayii* is more closely allied to *M. oreobates*, which is of the same size and also lives in the highlands, or to *M. variegatus*, a lowland species which has the same gorget colour as *lafresnayii*. The two highland forms may be independent derivatives of *M. variegatus*, *lafresnayii* arguably more recently so than *oreobates*, which is the justification for retaining *lafresnayii* as a subspecies of the Blue-breasted Bee-eater and keeping the Cinnamon-chested Bee-eater as a separate species without subspecies.

Still in Africa, the Red-throated Bee-eater (*Merops bulocki*) and the White-fronted Bee-eater (*Merops bullockoides*), inhabiting northern tropical and southern tropical woodlands respectively, and practically in contact with each other in Virunga National Park in north-east Zaire, comprise a classic example of a superspecies. They are both colonial cliff-nesters with well-developed systems of co-operative breeding, and their morphology and biology are all but identical. Both have a yellow-throated

morph, albeit rare in one population and very rare in the other. Basically red-throated, green and blue birds, they differ in facial plumage and in rump colour and spread-tail pattern. The significance of those parts of the plumage surely rests in visual signalling: the bee-eaters interact face to face, and they spread and tremble the tail when calling and spread it wide against the cliff face, using it as a support, when perched at the nest-hole entrance. The spread tail establishes the identity of a bird seen at a breeding cliff from a distance. Also significantly, these two species use the same array of call notes but utter them in different registers, so that the treble Red-throated Bee-eater and the bass White-fronted Bee-eater sound completely different from each other (see Voice). They have often been treated as two races of the same species, but the vocal and visual differences must ensure that they would never hybridize.

The Somali Bee-eater (*Merops revoilii*) is a white-throated, pallid version of the two red-throated species and is nearly parapatric with them; thus, its looks notwithstanding, it is probably quite closely related to them. Breeding parapatrically with all three is a striking bee-eater of the narrow, sandy, arid Sahelian zone from Mauritania to Djibouti and south to Lake Turkana in Kenya, the migratory White-throated Bee-eater (*Merops albicollis*). It is thought to belong to the *M. bulocki*/*M. bullockoides*/*M. revoilii* species group.

Böhm's Bee-eater (*Merops boehmi*) has a restricted range in south-east Africa, and its affinities are not obvious. By contrast, in the northern tropics, the Little Green Bee-eater (*Merops orientalis*) has a vast range, in eight subspecies, from Senegal to Israel and Yemen and from Iraq and Oman to Sri Lanka, Assam and Indochina. Depending on subspecies, the crown is green or rufous, the throat green, yellow or blue, the gorget wide or narrow, and the central tail feathers either a little or greatly elongated.

Another group of four species is composed of large, elegant, green, long-tailed arid-zone bee-eaters which are nearly parapatric in their distributions. These are the Blue-cheeked Bee-eater



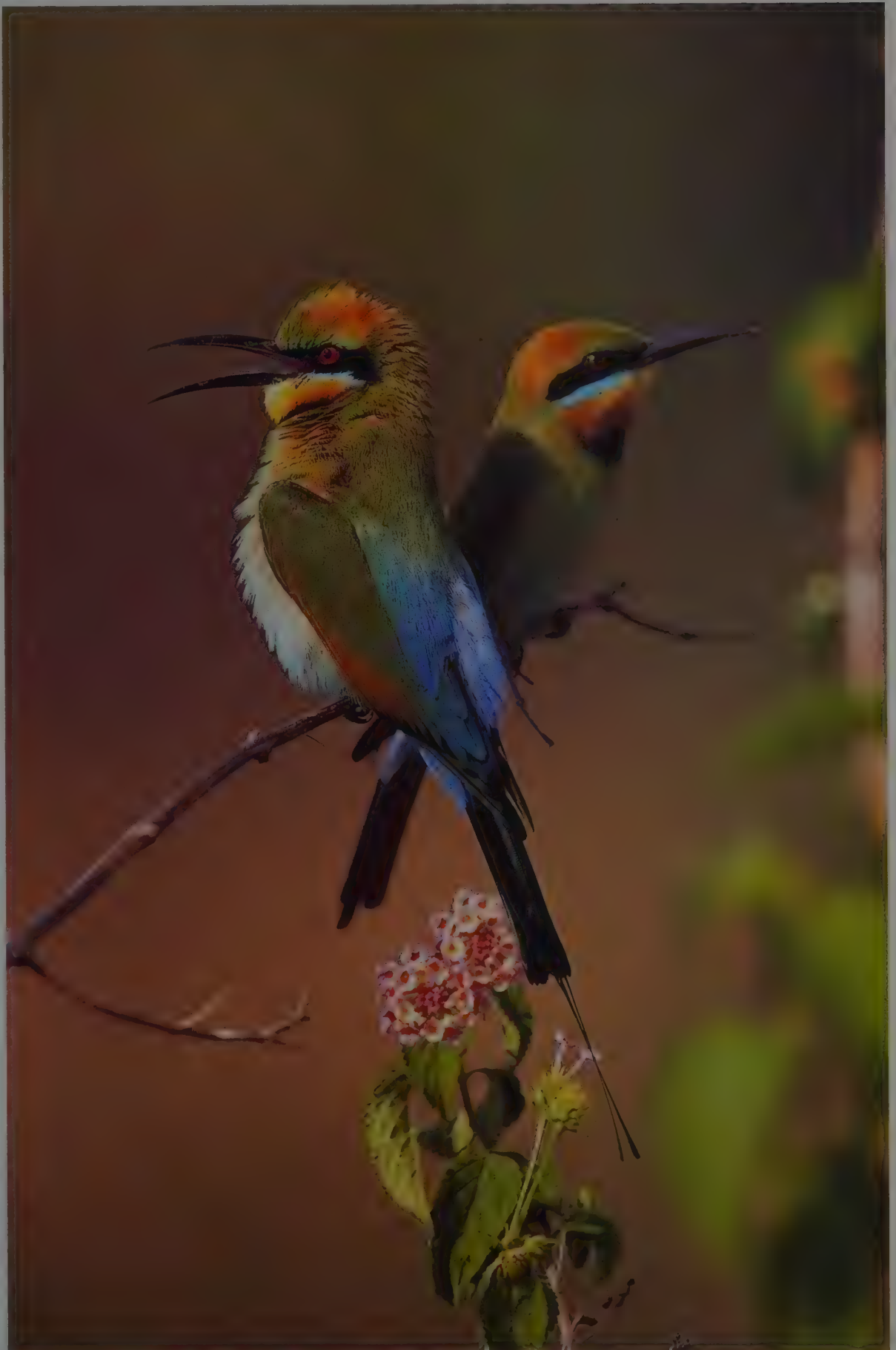
Bee-eaters might be considered a delicate version of kingfishers. Both groups are large-headed, short-necked and long-billed, but bee-eaters are more elegantly proportioned, with smaller heads and slimmer, more elongated bodies. Bee-eaters are notable for having gorgeous plumage colours, whether they are shy forest-dwellers or more conspicuous birds of open country. In the genus *Merops* the dominant colour tends to be green, although there are a few exceptions, notably two that are a dazzling carmine or rosy pink and one in which the ground colour is jet black.

A prominent feature common to most *Merops* species is a black mask, which varies in length and breadth with species, although posture too can influence the appearance of this patch. The long, slender, slightly decurved bill is common to all species, showing surprisingly little variation.

Sexual dimorphism is extremely limited in this family, with male and female generally indistinguishable in the field. One exception to this is the Rainbow Bee-eater, in which the male has long, very narrow tail-streamers with slightly spatulate tips, whereas the female has a much shorter, broader version.

[*Merops ornatus*,  
Australia.

Photo: Dave Watts]





Tail-streamers are present in a number of bee-eater species, but the tail shape of the Swallow-tailed Bee-eater appears unique within the family. In the past, this feature alone was used to justify the isolation of this species in its own genus, *Dicrocercus*. Nowadays, however, taxonomists generally agree that what appears to be a highly individual tail shape is really no more than an exaggeration of the fish-shaped tail present in several other species, notably the Little Bee-eater (*Merops pusillus*). As can be seen here, the sharp claws and long tails of the bee-eaters enable them to perch on vertical banks, in a style reminiscent of woodpeckers.

[*Merops hirundineus*  
*hirundineus*,  
Kalahari, Botswana.  
Photo: Joan Ryder/  
Gallo Images]



These Red-throated Bee-eaters, perched on a riverbank in northern Nigeria, illustrate one of the typical features of the Meropidae, namely the very short legs. The feet too are small and rather weak, although they carry long, sharp, hooked claws, which come into play during burrow excavation. A rather rare variant of this species occurs, in which the throat is yellow rather than scarlet; in northern Nigeria, it accounts for about 1% of birds. This form was originally thought to be a different species, and was named "Merops boleslavskii". Highly gregarious at all seasons, the Red-throated Bee-eater excavates its nesting tunnels in steep earth or sand walls.

[*Merops bulocki bulocki*, Komadugu Gana River, north Nigeria.  
Photo: P. Blasdale/Ardea]

(*Merops persicus*), occurring from west Sahara to central and south-west Asia, the Blue-tailed Bee-eater (*Merops philippinus*), which breeds from south-west Asia to New Guinea, the Olive Bee-eater (*Merops superciliosus*) of Madagascar and parts of eastern and south-west Africa, and the Rainbow Bee-eater (*Merops ornatus*) of Australia. All migrate to wintering grounds generally thousands of kilometres away, and accordingly they are long-winged. The first two are so alike that they have often been treated as subspecies of the same species, but in the north-west Indian Subcontinent their breeding ranges overlap in Punjab, India, and in Sialkot, Gujranwala, Gujrat and Jhelum Districts of Pakistan, without any signs of hybridization, and they are best treated as a species pair forming a superspecies. Olive Bee-eaters, with one subspecies breeding in Madagascar and patchily on the eastern African seaboard and another in desert in south-west Angola, are close relatives of the Blue-cheeked and Blue-tailed pair, and are considered to belong to the same superspecies, but instead of green, blue and yellow facial features they have olive and white ones. The Rainbow Bee-eater, smaller, more boldly marked, and with slight sexual differences, does not look very like the other three, which are nonetheless more likely to be its closest relatives than is any other species.

Three more are essentially Asiatic. The European Bee-eater nests from the west Mediterranean to about 70° E and also in South Africa, the Bay-headed Bee-eater (*Merops leschenaulti*) occurs in three subspecies from 70° E to mainland South-east Asia and Java, and the Blue-throated Bee-eater (*Merops viridis*) breeds in two subspecies from east China to Sumatra and from the Philippines to Java. Apart from the fact that the crown and mantle are chestnut-brown (green in juveniles) and the belly and tail greenish, the three do not have much in common and their systematic positions in the genus are difficult to appraise.

Lastly, there are two large, stunningly coloured species in Africa. The monotypic Rosy Bee-eater (*Merops malimbicus*) is a beautiful carmine and slate, and both subspecies of the Carmine Bee-eater (*Merops nubicus*) are equally striking in carmine and greenish-blue. Five other bee-eater species have scarlet and one of them also pink in the plumage, yet the vibrant rose-carmine of these two is unique within the family and very rare among birds in general. The Rosy and Carmine Bee-eaters have different voices and different bill profiles, the latter probably related to their specialist diets: the Rosy feeds on ants and bees, and the Carmine on locusts and bees. Similarities between them are that they feed aloft in continuous, wheeling flight, and they nest in dense colonies in sandy riverine places. They may be distant sister-species, but their relationships with other bee-eaters are obscure.

Most ornithologists in southern Africa regard their Carmine Bee-eater as specifically different from the northern population, treating the two as, respectively, *M. nubicoides* and *M. nubicus*. The two populations barely differ in voice or behaviour, but they do have different throat colours, tail lengths and body weights. How they might interact must remain speculative: their ranges are distinctly separate. If they are to be recognized as distinct species, then the Blue-headed, Blue-breasted, Little Green, Bay-headed and probably Blue-throated Bee-eaters should each be sundered likewise.

### Morphological Aspects

Arguably, bee-eaters are better proportioned than some other coraciiform birds, mainly because they are not quite so large-headed as the kingfishers, rollers and others. They have a moderately long, hard, sharp-pointed bill, decurved, with the culmen more curved than the gonys, and with sharp biting edges. The bill can open no wider than about 30°. Its sharp points are not used for stabbing prey, but with quite a strong bite the maxilla and the mandible function like forceps, enabling the bird deftly to pick an insect out of the air, seizing it in the very tip of the bill. The edges of the jaws are not serrated but are sharp and rigid, transmitting power from the jaw muscles to the bill tip, where small insects are crushed. Larger ones are carried one at a time to a hard perch, where, still held in the bill tip, they are immobi-



lized and partly dismembered by beating. The left and right rami of the mandible are strengthened by a shelf of bone which meets its fellow in the mid-line, back to a point below the forward edge of the nostrils. So astutely does the bee-eater handle an insect that only rarely is one dropped, and even then the bird retrieves it before it has fallen a metre.

In most species, the iris is brown, red-brown or red, and the eye is set at the side of the head so that vision is monocular, possibly with some overlap between the two lateral fields of vision directly in front. To what extent, if any, the birds rely on stereoscopic vision when hunting is not known, but a perched bee-eater will often tilt its head to scan upwards for prey or the presence of a predator, which suggests that a single optic field suffices for the detection of movement, even if distance may be better gauged binocularly.

The wing shape of bee-eaters varies from round-ended to pointed, and there is quite a striking correlation with foraging behaviour and migratory distance. Species that inhabit forest, as well as small bee-eaters living in reeds and among lush bushes and tall grasses, tend to be sedentary, territorial, solitary breeders and to forage locally, making short sallies after flying insects from perches in the vegetation; they have short, relatively rounded wings. They launch themselves into the air decisively and pursue prey in direct, non-undulating flight with rapid, even wingbeats, followed by a steep banking glide or quick twisting pursuit to seize the insect, a rapid change of direction, and a leisurely return to the perch with lengthy glides and slight undulation while flapping. Bee-eaters rarely hover, and then only momentarily. Those species inhabiting high latitudes or, in the tropics, open country such as broad river valleys, plains, arid savannas and desert edges are colonial nesters which must perforce seek their food far afield. They are strong fliers, they forage sometimes in continuous flight without bringing every prey item to a perch, they are mostly long-distance migrants, and they have complete mastery of the air. With wheeling and gliding flight on long, pointed wings, and with fast twists and turns in the chase or slow pursuit, they are accomplished aerial hunters, in addition to which they make beautifully controlled glides to drink, or a plunge to bathe. A particular curiosity that has not yet been investigated, nor until now even commented upon, concerns the primary coverts: in at least some bee-eater spe-

cies, the European Bee-eater being an example, the primary coverts do not lie in the usual manner on top of the primaries but are intercalated, with each covert half-tucked under its primary feather.

The neck is short, the tarsometatarsus or lower leg very short and somewhat fleshy, and the foot small, weak, brownish and dry-looking, not fleshy, with the outer two toes united basally and the three forward-pointing toes incapable of spreading on the perch, and with small, sharp, curved claws. On the ground, and sometimes when perched on a branch, bee-eaters are pigeon-toed, the foot pointing not straight forwards but a little inwards. Adapted for aerial life almost as strongly as are the swallows (Hirundinidae), bee-eaters do in fact quite often come to the ground, where the gait is a shuffle, the soles barely leaving the substrate. A bird may stay on the ground for half an hour, sun-bathing, preening, or fiddling with fragments, but it will seldom move more than a few centimetres in a minute. In the confines of the nest-burrow, however, a bee-eater shuffles surprisingly rapidly on its short legs, in a crouching position, covering the one or two metres of the burrow's length in only a few seconds.

In some species at least, the thighs are thinly feathered and in part featherless, and the pink skin shows through. The European and Blue-throated Bee-eaters sometimes dangle their legs in flight to expose the thighs, an effective way of dissipating heat and reducing heat stress.

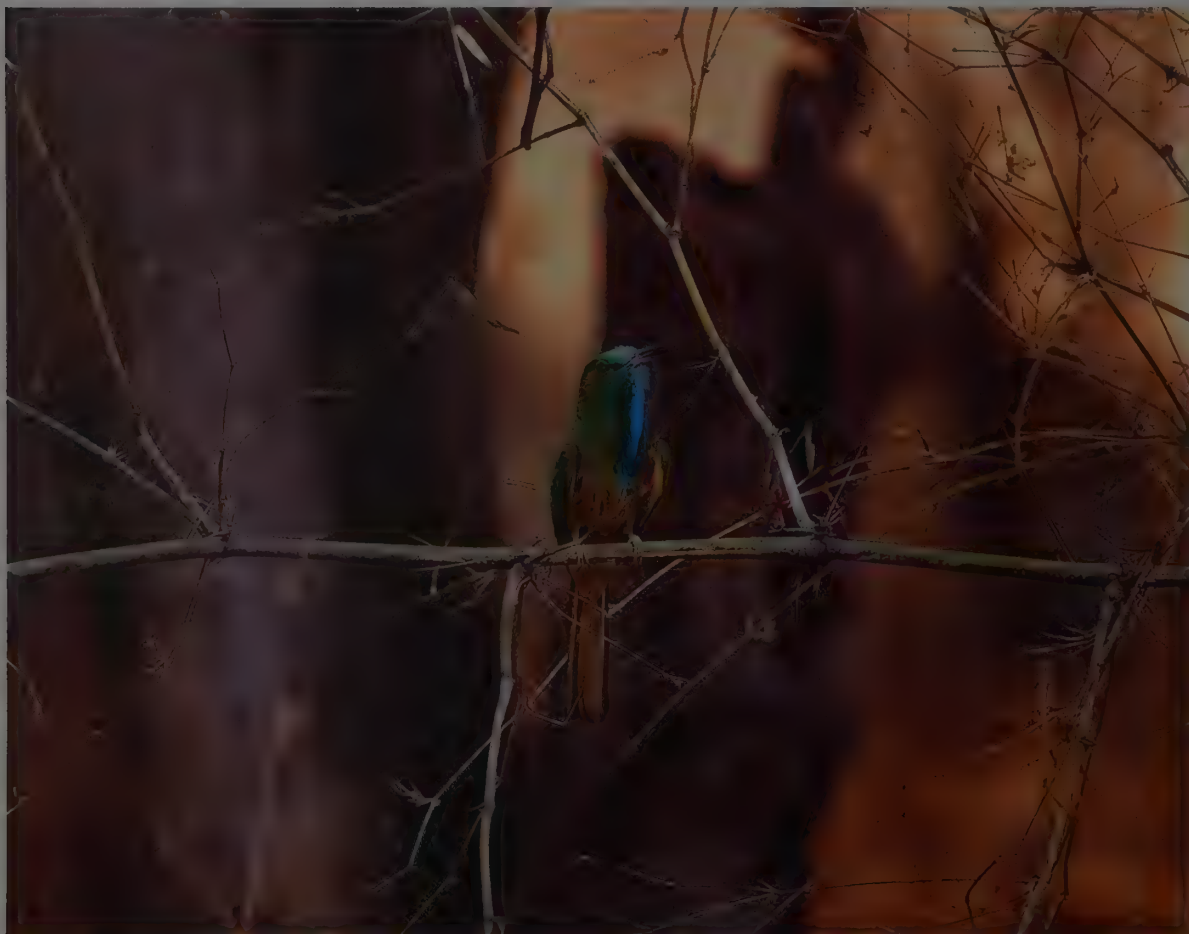
Besides perching and ground locomotion, the leg has one more crucial function: that of digging. When making its nesting-burrow and egg-chamber, the bird dislodges hard, compacted sand or earth by stabbing with its bill. Then, when the loosened soil needs to be cleared, the bird supports its weight on the tripod of its "wrists" and bill tip, and uses both legs to scabble soil backwards: using a sort of bicycling action, it kicks the soil for 30-50 cm, creating a little heap in front of a nest-hole entrance in flat ground or a fine talus below a cliff site. When a nest-hole is

in the process of being excavated, one can often see a pulsing spray of dusty soil emerging for up to three seconds at a time. It is a most effective method of digging.

Aside from its colours, the bee-eaters' plumage is not very remarkable. Some species have rather stiff and pointed forecrown feathers; others have stiff, red chin and throat feathers with non-radiating barbs, or long, soft, semi-pendent throat feathers. All have the ability to raise the upper mantle feathers at a steep angle, a distinctive trait of bee-eaters when they are sunning themselves. The tail, of twelve feathers, is rather narrow, and square-ended or a little rounded, and in many species the central pair of feathers are elongated, often greatly, into narrow streamers. In Böhm's Bee-eater, race *mentalis* of the Blue-headed Bee-eater and race *americanus* of the Blue-throated Bee-eater, as well as male Rainbow Bee-eaters, the streamers expand at the tips into tiny spatulae. This makes them more conspicuous from afar when a perching bird wags its tail a little forwards and backwards, something that all bee-eaters do habitually. Streamering of the tail is not connected with aerodynamic efficiency, but it promotes long-distance interspecific or intersexual recognition. One species, the Swallow-tailed Bee-eater, achieves the same effect by having not the inner but the outer tail feathers elongated.

Young Blue-bearded and Red-bearded Bee-eaters are all green. In the genus *Merops*, juvenile plumages do not generally differ much from adult ones, although juveniles do not have tail-streamers; nor, with the exception of the White-throated Bee-eater, do they have a black gorget. Young Black-headed, European, Bay-headed and Blue-throated Bee-eaters have a mainly green crown and hindneck, and young Carmine Bee-eaters are brownish.

In several species, the iris seems to be red in adult males but red-brown in females, and the males appear to have somewhat longer streamers than females, but only three of the 25 species exhibit any other sexual dimorphism or dichromatism. In Red-



The two members of the genus *Nyctyornis* are larger, heavier birds than the medium-sized *Merops* species. As can be seen on this Blue-bearded Bee-eater, the body is noticeably plumper, the tail long, square and streamerless, and the bill more robust. Wing shape is rather short and rounded, typical of sedentary birds that make short foraging sallies. The young are entirely green, whereas the juvenile plumages in *Merops* scarcely differ from the adults'. The most striking feature of *Nyctyornis* is undoubtedly the beard: the long colourful throat feathers that droop down shaggily or are puffed out as the bird calls.

[*Nyctyornis athertoni* *athertoni*, Bandhavgarh National Park, Madhya Pradesh, India. Photo: Joanna Van Gruisen/Ardea]



Bee-eaters are mostly strong, accomplished fliers. This is especially so for those species of open country, which often have to travel considerable distances in the normal course of foraging. The White-throated Bee-eater is an intra-African migrant, breeding in arid zones, yet, remarkably, moving to forested areas for the non-breeding period. It shows the rather long, pointed wings typical of a migrant bird, and also has a long tail, with particularly long streamers.

This remarkable sequence gives a slow-motion insight into details of the flight action.

[*Merops albicollis*.  
Photo: Stephen Dalton/  
CD Gallery]



bearded Bee-eaters, the feathers behind the nostrils are pink in males and red in females; male Rainbow Bee-eaters have long, slender streamers and females short, broad ones, males also having a bronzier hindcrown and a blacker gorget; and male and female European Bee-eaters show slight colour differences in many parts of the plumage. It may be significant that the two most dimorphic species are among the few bee-eaters that breed at high latitudes. Dimorphism is a product of sexual selection. Sexual selection is probably more intense in migratory, high-latitude species, which must compete to establish or re-establish pair-bonds every year, than it is in largely sedentary tropical ones that live in pairs throughout the year.

## Habitat

Bee-eaters are skilled and specialized predators of bees and a vast array of hymenopterans and other insects, all taken on the wing. It is rare for a bee-eater to eat grounded insects. The prime habitat requirements are, therefore, a plentiful supply of flying insects along with open airspace where these can be seen and pursued. Only a single species lives inside a "closed" habitat. This is the Blue-headed Bee-eater, an inhabitant of rainforest in West Africa and the Congo Basin, where it nests in tunnels which it makes in the soil. This forest-dwelling bee-eater forages within a few metres of the ground; it fly-catches in rather poor light, but in places where there is sufficient uncluttered airspace between leafy tangles, vines and the boles of large trees for a bird to succeed in catching its prey in more than half of its short sallies, as documented by T. M. Brooks and J. N. Kirathe.

At least six other bee-eaters, the Black-headed, Black and Rosy in West Africa and the Blue-bearded, Red-bearded and Purple-bearded in South-east Asia, are closely associated with evergreen forest but hunt in open airspace. They catch their food at the forest edges, at the sides of emergent crowns or of trees bordering windfall gaps, forest rivers and roads, or by tall trees overlooking forested hillsides and ravines.

Warmth is a key factor, and no bee-eater will tolerate daytime temperatures much below 21°C for any sustained period. Some of the larger species can survive freezing temperatures at night for a week or two, so long as it is hot enough during the

day to encourage insects to fly in profusion. The bee-eaters' love of heat, or rather of the insect life that heat generates, means, however, that the family is, with only a few exceptions, thoroughly tropical. The great majority of species inhabit bright, sunny places in low-lying country. They perch out in the open for most of the day, sometimes resting in lightly shaded places under a leafy canopy, and the several desert species live practically unshaded in extreme heat and insolation that would damage many other animals. Little Green Bee-eaters in Oman, for example, live among small stands of thorn trees in wadis in stony, waterless steppe where air temperatures are regularly up to 45°C, day and night, and occasionally reach 50°C: a bright, dry climate insufferably hot for people. The bee-eaters may seek shade in such extreme heat, and they often pant with the bill open, but they do not seem to be otherwise incommoded. They obtain their water needs from their insect food, and do not drink. Although the ground temperature can exceed 60°C, the nest-chamber itself, quite deep below ground, is much cooler. In a study of European Bee-eaters nesting in Spain, F. White and colleagues found nest-chamber temperatures to be rather uniformly about 25°C, when ground-surface temperatures fluctuated between 13° and 51°C. At the southern border of the Sahara, White-throated Bee-eaters nest in holes in burning hot, white sand with only a few clumps of dry herbs and the occasional dead-looking bush; they hunt from whatever perch is at hand, a fence perhaps, panting a lot when they perch and sitting with the body held high to shed heat from the featherless inner sides of the thighs.

This may seem to be departing from the conventional meaning of "habitat", yet bee-eaters spend such a high proportion of their daytime lives in flight or at an elevated perch in the middle of airspace, where almost any substrate will do for a lookout perch, that air is their habitat. In a study of energetics of three tropical bird species, D. M. Bryant and C. J. Hails found that, by day, Blue-throated Bee-eaters spent 21% of the time flying and 71% perched on the lookout for food; the remaining 8% of daylight hours were passed at the nest or in preening, sun-bathing and water-bathing.

To treat habitat in the usual topographical and vegetational terms, one or another bee-eater species lives in most warm Old World landforms. None is confined to a type of vegetation dominated by one or a few plant species, in the way that Blue-bel-



Undoubtedly the best-known and most studied member of the genus *Merops* is the European Bee-eater. It is also one of the most representative, showing many features common to them all, especially when seen flying freely high in the sky. The body is slim, the plumage strikingly multicoloured with the face and sides of the head strongly patterned. The tail consists of twelve feathers, the central pair elongated into short but sharply tipped streamers. The wings, long, fairly broad and pointed, with a thick dark band along the trailing edge, testify to the lifestyle of this species, a long-distance migrant capable of flying more than 500 km in one day. On the other hand, its feeding habits demand great mobility. Sometimes hunting by sallying forth from a high perch, more often it feeds in continuous flight high in the sky, alternating a graceful wingbeating action with moments of sudden acceleration and of skimming through the air on outstretched wings.

[*Merops apiaster*,  
Sohar, Oman.  
Photos: Hanne & Jens  
Eriksen (above);  
Hanne & Jens Eriksen/  
BBC Natural History Unit  
(below)]



Most bee-eater species live in open, sunny savanna country where they perch conspicuously and can fly freely in pursuit of insects, but a few are associated with more wooded habitats.

Among these is the Red-bearded Bee-eater, which inhabits lowland evergreen forests in South-east Asia. It often hunts from a half-concealed perch in the middle storey, beside a clearing or a streambank, where sufficient air space allows for insects to be easily spotted and captured. The scarlet forecrown and reduced area of pink on the central crown indicate that this bird is a female.



[*Nyctyornis amictus*, Fraser's Hill, Malaysia. Photo: John Holmes/FLPA]

As flying insects abound near water it is not surprising that several bee-eater species establish their living quarters in its proximity. One such is the Blue-breasted Bee-eater, the lowland races of which show a preference for marshes, swamps, reedy lakeshores and grassy hillsides. As a solitary breeder, it is not reliant on high banks for nesting sites and often excavates holes in sloping ground near lakeshores or on hillsides.

[*Merops variegatus* variegatus, Ekwata, Gabon. Photo: Josep del Hoyo/Lynx]

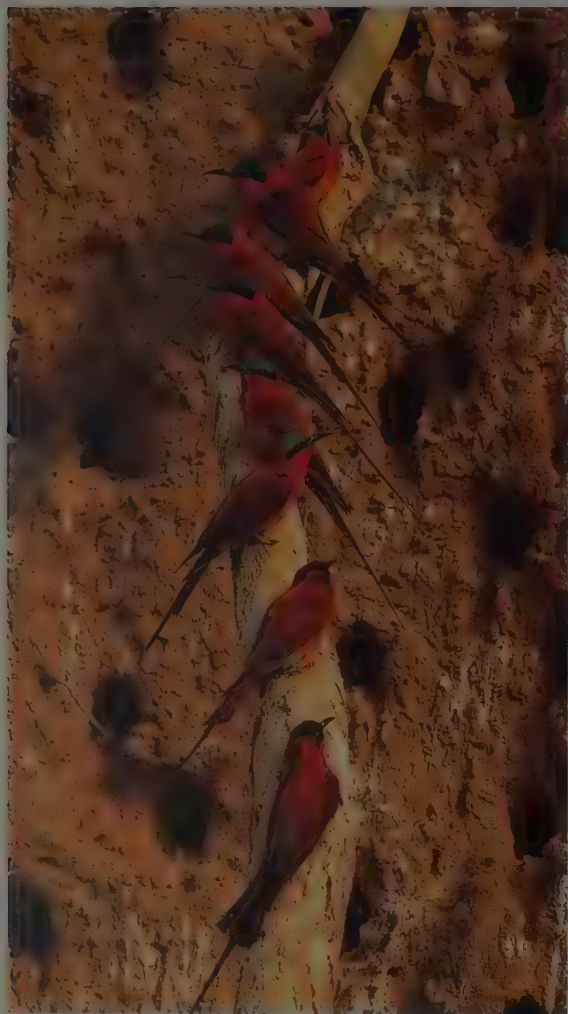
lied Rollers (*Coracias cyanogaster*), for instance, are confined to *Isoberlinia*-dominated African woodland. As already mentioned, a quarter of bee-eater species are restricted to African or Asian evergreen lowland forest zones, most inhabiting forest edges and tops and only one living deep in gloomy forest. They are mainly sedentary, and are unlikely to occur in areas without suitable nesting sites. Most forest-zone bee-eaters make their nest-holes inside the forest, in a low bank or other place where a few square metres of ground with earth of the right texture for excavation are free of herbs. Black-headed Bee-eaters forage at the edges of forest or in open canopy, but nest in more open situations such as a grassy slope 80 m from the edge of gallery forest, as F. Dowsett-Lemaire and R. J. Dowsett found in south Congo. Since "forest" bee-eaters nest solitarily or in loose aggregations, a large area of vegetation-free soil is not needed; indeed, it will usually be avoided. An exception is the West African Rosy Bee-eater. This species ranges in the forest zone and in adjacent humid, well-wooded savannas, where it gathers in vast, dense colonies to nest in sandbars exposed by the falling waters of broad rivers. It forages immediately above the canopy of dense riverbank forest, and after breeding disperses or migrates for several hundred kilometres, to spend the off-season feeding over the tops of forest and mature savanna-woodland trees. The nest-site is a gently shelving sandbar, bare but for a thin growth of sedges and annuals. One colony occupied a hectare of bare, flat sand, with two nest-holes per square metre, so there would have been at least 20,000 birds before breeding. Other colonies are thought to have numbered 25,000 and 50,000 adults. The most aerial of all bee-eaters, Rosies may well fly daily 10 or 20 km from the vast colony to find food. For the ants and bees that they feed upon, the tropical-rainforest/savanna-woodland interface may be one of the most productive terrestrial habitats in the world; yet it could take a patch of it 40 km wide to sustain that multitude of birds.

Little Bee-eaters are partial to drying-out marshes with waist-high grasses, reeds and sedges interspersed with *Mimosa*

*pigra* bushes and other woody growth. In the dry season in Nigeria, they occupy marshes and grassy lakeshores and streamsides; in the rainy season, when their young fledge and disperse, they live in cultivated land, grassy clearings in woodland and forest, bushy dunes, and rocky outcrops with clumps of elephant grass, as well as on treeless grass plains. They hawk for insects from the middle or the top of a long grass stem.







flying out for a few metres low over open ground or metre-tall growth, and often keep watch from the side of a tree or occasionally from its crown 20 m up. A favourite nesting micro-habitat is the burrow of an aardvark (*Orycteropus afer*), where the bird makes its own burrow in the roof.

Of the Little Bee-eater's close relatives, the Blue-breasted inhabits reedy lakeshores, beds of papyrus and reedmace (*Typha*), rank grasses in swamps, wet forest glades, cattle pasture, and steep grassy hillsides. Cinnamon-chested Bee-eaters are birds of wooded hillsides, upland forest edges and clearings overgrown with bracken and elephant grass, and gardens, at altitudes of around 2000 m: they nest in embankments, earth cuttings, quarries and tall cliffs in sunny places. Swallow-tailed Bee-eaters are more arboreal, inhabiting mature lowland woods dominated by *Isoberlinia*, *Baikiaea*, *Colophospermum*, *Brachystegia* or *Combretum* trees; they are somewhat migratory, dispersing or wandering seasonally over considerable distances, using thickets, parkland, plains and *Acacia* semi-desert.

Most other species occupy the same mixture of woods, cultivated land and grassy places, often near water and human habitations, in Africa, tropical and subtropical Asia and Australia. Colonially breeding species require tall earthen cliffs, as does Africa's Red-throated Bee-eater, or expanses of sandy soil, the typical habitat of Asia's Blue-throated. Whether sedentary like the former or migratory like the latter, such colonial birds tend to use the same site year after year. Apart from the nesting requirement for earth banks or undisturbed flat sandy ground, the breeding and non-breeding habitats of most migratory bee-eaters are similar. A notable exception is the White-throated Bee-eater, which breeds in sandy Sahelian savanna from Mauritania to Eritrea, south to Djibouti and Lake Turkana, and then migrates a thousand kilometres to the south or south-west to spend the off-

season in and near the coastal and equatorial rainforest zone. There it lives for several months, mainly by exploiting flying ants above the forest canopy.

Summer and winter habitats of bee-eaters that move intercontinentally are usually similar, but sometimes dissimilar. European Bee-eaters, for example, breed north to the 21°C July isotherm, which takes them north to about 57° N to the east of Moscow, and live in broad river valleys, pasture and cultivated land, well timbered or with scattered trees, on sunny hillsides and plains, along shrubby riverbanks, and in open landscapes with cork oak woods, olive groves, tamarisks, cereal fields, flowering pasture, and Mediterranean macchia, the last habitat consisting of dense, low, aromatic bushes. Spending the non-breeding season in tropical western and south-eastern Africa, they avoid dense evergreen forest and also desert, and occur over grassy and wooded savanna, plains, steppe, lakeshores, large river valleys and timbered farmland, from sea-level up to 2250 m and occasionally to 3000 m. On their Central Asian breeding grounds, Blue-cheeked Bee-eaters inhabit steppe and salty semi-deserts with low dunes, and arid dissected country with thin pasture and canals, as has been shown by surveys carried out in the early 1990's by E. M. Belousov and S. M. Kossenko: the same birds in Africa shun deserts, and spend the non-breeding season there hunting widely over open bushed grassland, cultivated light woodland, swamps, reedy lakeshores and mangroves.

Although bee-eater habitats include lakeshores, reedbeds, swamps, mangroves, streamsides, river valleys and river sandbars, expanses of water are not essential for them. Flying insects abound near water, so bee-eaters often forage in watery habitats, even though they are quite capable of satisfying their food and dietary-water needs in waterless regions. They bathe when they can, but are not incommoded if they cannot. Earthen banks, especially those by streams that seasonally cut themselves away to create clean, plant-free cliff faces, are favoured by many species for their nesting burrows, yet bee-eaters remain thoroughly dryland-based birds.

## General Habits

All bee-eaters are diurnal birds, and their feeding activities are restricted to periods from well after dawn to well before nightfall. They migrate by day, but European, Blue-cheeked and Rainbow Bee-eaters also migrate on moonlit nights, where a crossing of the seas or hostile terrain takes them longer than the available daytime hours. Over a period of nine years, T. J. Roberts recorded 28 spring arrivals of flocks of Blue-cheeked Bee-eaters on the Pakistan coast, most of these occurring in the midnight hours and only three by day.

They are also very social birds, and even those that nest in solitary pairs have an individual distance of zero. In other words, the male and the female commonly perch side by side, the second alighting within a few centimetres of the first, and both make quick little sideways steps until they are touching or pressing each other's side. Likewise, parents sit touching their offspring, all six or seven birds sometimes packed together on a twig, facing the same way. In trees, they habitually roost in that manner on an inner leafy twig, at dusk animatedly turning their heads this way and that and after nightfall shuffling even closer together, fluffing out the plumage, burying the bill in the back and closing their eyes to sleep.

Sociability is enhanced in several of the non-forest bee-eater species by breeding coloniality, the density and size of colonies varying among species. Black Bee-eaters tend to nest solitarily, but in Sierra Leone and Liberia they form small colonies with half a dozen nest-burrows, and the birds seem to remain gregarious throughout the year. White-throated Bee-eaters are highly gregarious outside the breeding season, migrating in flocks, and foraging in loose aggregations in which an individual may be in visual or vocal contact with 50 or more others all day; they breed colonially, but the nests, the great majority of which are each attended by five or more adults, are mostly 30 m apart. Cinnamon-chested Bee-eaters keep in small flocks all year, these com-

*Apart from the few forest species, most bee-eaters are markedly social birds, although the degree of sociability varies considerably. The most gregarious species are the spectacular Rosy (Merops malimbicus) and Carmine Bee-eaters. The Rosy nests in vast colonies on the sandbars of large West African rivers and winters gregariously in rainforest areas, while the Carmine forms large, compact breeding colonies, mostly in sand cliffs along large rivers, the same sites being used year after year. Outside the breeding season they forage in smaller flocks, but roosts may number hundreds or even thousands of birds.*

[*Merops nubicus nubicoides*, Okavango River, Botswana. Photo: Art Wolfe]



Bee-eaters in general have a strong social sense. This is most highly developed in those species that breed colonially and have evolved a complex social structure going beyond the family to include helpers and clans that not only live together at a breeding colony but may also form foraging and roosting flocks during other seasons. Even non-colonial breeders appear to manifest a certain desire for physical contact. When the members of a pair alight, they perch side by side, the last one to arrive side-stepping quickly until it is touching or pressing closely against its mate. Nowhere is this habit of clumping seen more clearly than in family groups, such as those formed here by Little and White-fronted Bee-eaters, where all the individuals sit huddled together, typically facing the same way. Many species of bee-eater roost communally in this fashion in trees. They arrive at the roosting site before dusk, after which side-stepping movements and roosting calls continue until all is quiet. There may be renewed bouts of shuffling, bringing the birds ever closer together in tightly packed rows, until all are composed comfortably for sleep. Such clumping also takes place during the day when the weather is cold.

[Above: *Merops pusillus argutus*,  
Okavango River,  
Botswana.  
Photo: Art Wolfe.



Below: *Merops bullockoides*,  
Pilanesberg, Mpumalanga,  
South Africa.  
Photo: Heinri van den Berg/  
Bios]



Aggressive bee-eater behaviour, as seen in these Blue-tailed Bee-eaters, is seldom recorded on feeding territories, but it is commonplace at roosts and colonies. Mainly harmless bickering, which seldom leads to a more serious dispute, it typically occurs between a perched bird and another, either perched too or intending to perch. Birds landing at some distance and approaching by degrees are less apt to provoke a threat or an attack, but an aggressive individual may react to the new arrival by lunging forwards with bill wide open, wings raised and tail fanned. The threatened bird may react by leaning towards the aggressor and gaping silently.

[*Merops philippinus*, Sundarbans, Bangladesh. Photo: Gertrud & Helmut Denzau]

posed of two to five pairs and their families. Little Green Bee-eaters nest solitarily or in loose or dense colonies, European Bee-eaters usually in small but dense colonies, Blue-throated and Carmine in large, dense colonies with several hundred nest-burrows, and Rosy Bee-eaters in colonies of tens of thousands. The most densely colonial species tend to be those whose nesting sites are scarce or localized, and another correlate is the degree of territoriality. The Blue-throated, Carmine and Rosy Bee-eaters are barely territorial at all, although a bird at its nest-burrow

entrance will lunge aggressively at a neighbouring hole-owner 20 cm away. Rainbow Bee-eaters are highly territorial when nesting, pairs defending adjacent territories which are polygonal, with a tree at each corner.

Red-throated and White-fronted Bee-eaters have attracted a great deal of research interest, in Nigeria and Kenya respectively, on account of their social structures, which have been described as among the most complex of any bird species anywhere in the world. They are highly sedentary birds, and they breed in compact colonies. Adjacent colonies, several hundred metres apart, have little to do with each other, although a few young or unpaired birds may change allegiance each year. Each colony is divided into a number of clans, a clan comprising two or three pairs, helpers and offspring. Densely clustered nest-burrows on a cliff face are dug by the birds well in advance of breeding, and are used for roosting for weeks afterwards; indeed, the lives of the individual bee-eaters in the colony centre on their nesting cliff for the entire year.

Helpers are generally the sons, now adult, of the long-lived pair which they are helping with nest duties. In successive years, they may alternate between helping and siring. Paternity is difficult for researchers to establish, and so is even maternity, since the clan's sociosexual structure is not so comfortable as at first appears, and within the clan and the colony there is much opportunistic sexual infidelity. A male spends much time guarding his mate from the attentions of other males, yet he himself loses no opportunity to rape another female, who is quite capable of exploiting inattentiveness of adjacent nest-owners to lay an egg in their nest for them to foster. To cap it all, one or two individuals in some colonies are robbers, birds that find it more rewarding to steal an insect from an incoming neighbour than to go out hunting themselves. These two bee-eater species, the Red-throated and White-fronted, thus have four tiers of social kinship: the pair, the family including some "adoptees", the clan, and the colony.

With all of its human-like complexities, the clan remains more or less intact for long after breeding has finished, and all through the year the daily regime is characterized by strong bonds between the pair-members and within the extended family. A typical day begins with the colony emerging from the nest-holes soon after dawn. For half an hour or so the birds perch nearby, on the cliff

Whether they live in watery habitats near lakes, by rivers or swamps, in savanna lands or semi-deserts bee-eaters are very seldom seen to drink since they obtain all the moisture they need from their insect prey. Though it is not a common activity or form of comfort behaviour they do in fact bathe from time to time. Bathing is performed by gliding down to the surface of a large expanse of water and taking a shallow, dive in, head first, interrupting their flight only for a second. Here a European Bee-eater has returned to a perch after a bathe in a canal. It now proceeds to ruffle and shake its dripping plumage, before indulging in a thorough session of preening.

[*Merops apiaster*, Lleida, Spain. Photo: Jordi Bas Casas]





Bee-eaters are known to spend up to 10% of the daylight hours in comfort behaviour of some kind, aimed chiefly at keeping their plumage in optimum condition. These Blue-tailed Bee-eaters illustrate two of the postures typically adopted during periods of rest. One bird ruffles its feathers, enabling the air to circulate, and permit more efficient heat exchange. The second bird is going through some of its stretching exercises: after raising both forewings above the back with wrists almost touching, it now proceeds to stretch one wing at a time, both downwards and backwards, at the same time spreading wide that half of the tail which lies beneath the outstretched wing. In addition to the purely practical effects of such comfort behaviour, it undoubtedly also plays a social role as an important group activity, and is particularly widespread in the colonial species.

[*Merops philippinus*,  
Bellanwila, Sri Lanka.  
Photo: Ray Tipper]





As these two Blue-cheeked Bee-eaters sit in the late evening sun, one of them is caught in the midst of its pre-roosting comfort routine. Stretching is often accompanied by a bout of preening, in which the bird uses its bill to sort through the plumage, searching for any dirt, dead skin or parasites, and checking that the feathers are in tip-top condition. Preening is a vital part of normal body-care behaviour for all birds. Allopreening, with one bird preening another, has never been observed in bee-eaters.

[*Merops persicus persicus*,  
Hafeet, Oman.  
Photo: Hanne & Jens  
Eriksen]

top, on roots emerging from the cliff face, and on twigs and bushes; they preen, interact, change positions, call and bicker, and then, abruptly, all of the members of one subset or clan take flight and depart in a flock for the clan's feeding territory, usually about a kilometre away. Other clans depart in other directions almost immediately. The clan remains in its feeding territory all day, vigorously defending it against incursion by all other bee-eaters of the same species; but, if there are nests with young to be fed, there is a constant coming and going between colony site and feeding grounds. In the latter, the constituent pairs and helpers in the clan have different but largely overlapping foraging ranges. Feeding is punctuated by periods when many members of the clan, more or less at the same time, will rest, preen, sun themselves, and regurgitate pellets of indigestible insect remains.

In the late afternoon, the clan forgothers and flies back to its cliff site. The next hour, up to sunset, is a time of socializing, bickering, greeting, displacements, preening, some chasing and much calling. Typically also, many birds come down to an area of sandy or compacted lateritic soil, often immediately below the nesting cliff. There, each one picks up small fragments of snail shell, vegetation or grit, fiddling with and seeming to test it, dropping it, flinging it aside, or tossing it from bill tip into the throat and swallowing it. Soon after sunset, all members of the colony enter the nest-burrows to sleep, or fly to a thick clump of trees to roost there.

Clannish behaviour is never interspecific, so far as is known, although small Red-throated Bee-eater colonies are sometimes confluent with a large colony of Carmine Bee-eaters. European and Blue-cheeked Bee-eaters often nest in mixed colonies, where their interactions have been studied by S. M. Kossenko and C. H. Fry; these authors found a degree of interspecific competition at the individual level, but none is known to occur at the clan level.

A great many species of bird produce pellets of indigestible remains of their food, but in few is this a more obvious part of the daily activities than it is in the bee-eaters. Unless ants destroy the regurgitated pellets, the 2-cm black oblongs litter the

ground beneath the twigs favoured for loafing by day and roosting at night. Egg-chambers soon become a centimetre deep in trodden-down pellets, and in cliff-nesting species the nest-burrow and the ground below its entrance are often littered with blackish insect sclerites from broken pellets. The pellets do not give off an odour, which suggests that, after digestion, there is very little organic matter remaining in them other than sclerites, which do not rot. They are readily collectable, for the purposes of analysing diets, and, if the ground is cleared and further collections made, it is easy to date them for the study of seasonal changes. Tiny head capsules of ants and minute leg or antennal sclerites appear in pellets, and it is believed that pellets are a highly reliable indication of what a bee-eater has eaten, provided, of course, that all significant sclerites can be found and identified. A bird coughs up three to six pellets a day and probably just a single one at night; each is regurgitated about two hours after a good bout of feeding commences, as A. Christof has found with European Bee-eaters in France. A pellet generally contains about twelve middle-sized insects, or up to 100 very small ones.

As much as 10% of daylight hours may be spent in a variety of comfort activities: sunning, dust-bathing and water-bathing. In hot weather most bee-eaters commonly pant, and if it is very hot some of the larger and more aerial bee-eaters, when in flight, thermoregulate by letting their legs hang down, exposing the pink-skinned thighs to evaporative cooling. Sunning takes place at odd moments throughout the day, and involves three basic postures. Much the commonest is the raising of a side-to-side row of mantle feathers, generally when the bird is perching with its back to the sun; in side view, the hindcrown is then seen to be peaked, the nape feathers compacted, and a deep cleft driven between the raised feathers and the sleeked or less raised back plumage. Quite often, when the sun is overhead, a perched bee-eater extends its neck to one side in what is termed the "broken-necked" posture, and closes its eyes, pants with the bill open, and ruffles the feathers on the upper side of the neck. The third sun-bathing posture is usually seen in the late afternoon: a bird on a warm sunny bank slumps its body on to the soil, spreads the wings and



tail so that they rest on the surface, ruffles the marginal and lesser wing-coverts, retracts the neck and points the bill straight up, holding the position for minutes at a time. Among the colonial bee-eaters sun-bathing is a social activity, and several individuals adopt the same posture at once.

Water-bathing is not very common, and is invariably performed by gliding down towards the still surface of a large body of water and making a little head-first dive, with only a momentary check in flight. Generally, the bather returns to a nearby perch to preen and shuffle its plumage, and it may carry out two or three splashdowns and preening sessions in succession.

## Voice

*Merops* bee-eaters are vocal birds, pairs and flocks calling frequently when foraging and migrating, and making softer and more conversational noises in the nest-burrow and when loafing out of it. The contact calls of most species have a strong generic similarity, a pleasant-sounding, rolling, far-carrying "prruip" or "pruuk" in the case of the European Bee-eater, and a dry, fast, rolling "tree" in Little Green Bee-eaters, for instance. The most diminutive species, the Little Bee-eater, utters a quiet, rather high-pitched "kreee-kree" or sibilant "tseep" or "tse-ip", and the largest one, the Carmine Bee-eater, gives a short, rather guttural "graa" or "tunk" or "raak". Notes may be given singly, but they are often repeated once, as with the European Bee-eater's "pruuk-pruuk", or up to about six times, as is the case with the Carmine Bee-eater's "tunk, tunk, tunk, tunk, tunk, tunk". Pairs of birds often call reciprocally, and in a loosely knit flock contact calls tend to be answered immediately, resulting in a surge of noise. Individuals in a colony tend to call all at once, and en masse a thousand Blue-cheeked Bee-eaters make a far-carrying, rolling, melodious and gladsome medley with a purring quality and almost a beat as excitement mounts and wanes every few seconds. The voices of the two *Nyctyornis* bee-eaters are more roller-like than *Merops*-like, and include a



gruff "quo-qua-qua-qua-qua", a deep "kwow", and hoarse, guttural croaks and chuckles.

Although the main calls seem to be rather simply structured, short and almost monosyllabic, sonographic analysis or a good ear reveals a range of subtle inflections, and individual and gender differences in some calls of European Bee-eaters have been identified. Aside from the commonest or main call, usually interpreted as a contact call between an individual and its mate or

During preening, the Rosy Bee-eater may use its bill in two ways: in a nibbling action with the bill open; or in a stroking movement with the bill closed.

The nibbling method is the more thorough, as the feather is worked upon moving from base to tip. Stripping, another form of nibbling, involves one or several feathers being pulled through the bill in a single movement.

Often employed to supplement nibbling, the stroking action is less effective, its main purpose being to apply preen oil or to smooth feathers down.

[*Merops malimbicus*,  
River Kaduna, Nigeria.  
Photo: C. H. Fry]

Because of their hole-nesting habits one acute problem for bee-eaters is the quantity of ectoparasites, mainly minute mites and flies, that infest their skin and feathers. These may cause lesions, help spread infectious diseases, and at least probably involve discomfort. Water- and dust-bathing, both activities practised by the European Bee-eater, assist in cleansing their bodies of these pests, and a certain amount of vigorous scratching of the head and chin, areas impossible to reach with the bill, may at least help to alleviate the problem of sudden irritations, if not necessarily eliminating the unwanted guests.

[*Merops apiaster*,  
Bárdenas Reales, Spain.  
Photo: José Antonio  
Martínez]





Sunbathing, or sunning, can be divided into different techniques. It covers sunbasking, when the bird absorbs heat from the sun to maintain its body temperature, thus reducing the need to expend energy; and sun exposure, when a bird positions itself in the full sun although it is not in need of extra heat. The basic function of sun exposure seems to be feather maintenance, particularly of those of the wing and tail, the areas a sunning bird exposes most. All bee-eaters commonly sit with their backs to the sun and the mantle feathers sharply raised and fanned. Certain species adopt a "broken-necked" posture, with the neck inclined acutely to one side, and the neck feathers on the other side fluffed out to receive the sun's rays. Alternatively, they may lie spread-eagled on flat or sloping ground near the nest-holes, with the wings fully extended and the tail fanned, at the same time panting and raising the mantle feathers. Such postures may activate the ectoparasites so that they become more accessible to the preening bird. They may also aid to increase the flow of oil from the preen gland, so noticeably stimulated in one of these Carmine Bee-eaters and also in this Little Green Bee-eater.

[Above: *Merops nubicus nubicus*, Central African Republic. Photo: Michel Gunther/Bios.



Below: *Merops orientalis cyanophrys*, Eilat, Israel. Photo: Alan Williams/NHPA]



family, or between members of a flock, no fewer than 14 other vocalizations are known for the Red-throated Bee-eater and 19 or 20 for the European Bee-eater. The vocalizations of those two species, and of the Blue-cheeked and White-throated Bee-eaters, have been studied in some depth in the field or the aviary. For the most part, however, the voices of other species are not at all well known, and the behavioural contexts in which they are uttered, in other words, the biological meaning of the various voices, remain very poorly understood.

Calls used by Red-throated Bee-eaters include a low "wip" in contact between perched birds; "weep, wit" in contact in flight; "tic-ic-ic-ic-ic" as warning, and flight intention; "tic-tic-tic" in alarm about a nearby hawk or large mammal and a short, treble, falling "prrrrr'ng" in alarm about a distant, high-flying hawk, the two alarms being quite different; in greeting, an excited cadenced trill, "trrrr-trrrr-trrr-trr-trr-trr-teu". They also have three different calls used for roosting intention, during copulation, and as courtship-feeding intention. On arrival at the nest-burrow entrance with food for the young, the adult utters a special food-delivery intention call, a repeated "prrrp" or "chrup"; on departure after food delivery at the nest, a soft "you" or "oop" is emitted. Three other calls are given: by adults encouraging nestlings to leave the nest, by nestlings when begging, and by juveniles soliciting food.

Functions ascribed to European Bee-eater calls are similar. These are low-intensity contact; high-intensity contact; summoning, and male carrying food to his mate; greeting, and appeasement; threat; alarm; anxiety; pain or extreme fear; courtship; a babbling call used by females to advertise themselves; copulation intention, by both sexes; a soliciting call by the female; a male copulation call; a nest call, used when a bird is excavating its tunnel, before nest-relief, and when a parent is bringing food items into the nest; roosting; and four separate nestling calls.

Red-throated Bee-eaters in the northern tropics of Africa look very like White-fronted Bee-eaters in the southern tropics. The two have been treated as a single species, and are surely closely allied and of recent common descent. Their vocabularies seem to be exactly the same, but the birds differ in one significant respect: the Red-throated has a treble voice and the White-fronted a deep, gruff, base one. To the human ear they sound completely

different, and it would be fascinating to study vocal and visual interspecific reactions in the only locality where the two are known to meet, Virunga National Park in Zaire. By contrast, the European and Blue-cheeked Bee-eaters are not particularly closely related within their genus, yet they, too, are similar in their vocalizations, and practice is needed to distinguish them vocally in the field. They often nest in mixed colonies, where each appears to react to at least some of the other's calls.

What is characterized above as the greeting call of European Bee-eaters is a clear ringing note, repeated several times and interspersed rhythmically with other notes; it lasts for 2-3 seconds and could almost be described as a song. Likewise, Little Bee-eaters have a high-intensity greeting or song, of a second's duration, a complex "siddle-iddle-ip d'jeee".

Altogether, it is clear that voice is of great import in the lives of the better-known bee-eater species, and doubtless it is among the less well-studied ones, too.

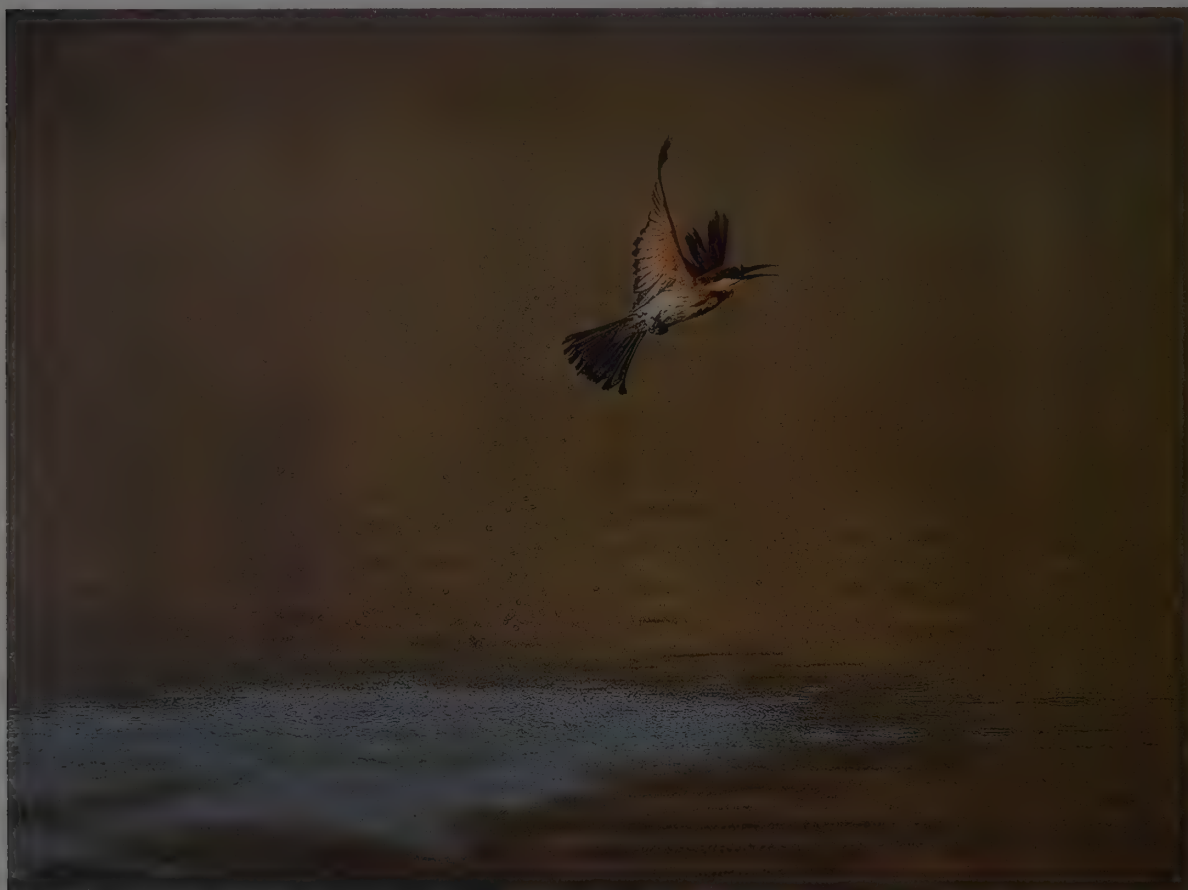
## Food and Feeding

Not a great deal is known about the two large *Nyctornis* bee-eaters. They hunt solitarily or in pairs from leafy perches overlooking some small clearing in hillside forest, making occasional sorties to catch a passing insect. In pursuit of prey they fly quite fast, twisting and turning nimbly between the treetops, then returning to the perch with undulating glides and brief flapping. Their hawking, however, lacks the verve and aerodynamic manoeuvrability of other species, and both the Red-bearded and the Blue-bearded Bee-eaters spend much time sitting quietly and stolidly for long periods, moving only to change position from time to time. They catch wasps, hornets, carpenter-bees, honeybees, dragonflies, cicadas, weevils, scarabs, passalid and other beetles, crickets, ants and termites, mainly in aerial pursuit, although they also take flightless arthropods such as woodlice, and may prove to feed on small insects taken in flowers. Large, hard, airborne insects, many of them 40 mm long, are carried back one at a time and beaten against the perch, the parts knocked off not being retrieved; in the case of some large beetles, only the abdomen seems to be eaten.

Courtship behaviour is generally unspectacular in the Meropidae, except in the case of the White-throated Bee-eater. When birds of this species gather in the evening, prior to roosting, an individual may indulge in a "butterfly" display in which glides with the wings held high alternate with shallow wingbeats. After "butterflying" it perches next to another with its wings raised. The latter responds by also lifting the wings, then, facing each other, they fold their wings and bob up and down. These performances, which may lead to copulation, begin before the birds have left their winter quarters and continue into the nesting period.

[*Merops albicollis*,  
Samburu, Kenya.  
Photo: Eric Woods/  
Oxford Scientific Films]





The Bay-headed Bee-eater seizes an opportunity to bathe. When some Merops are seen to splash down into water, their intention is not always clear, owing to the rapidity with which the action is performed. They could be simply bathing, or even diving for food: insects on or below the surface. Observers have frequently insisted that bee-eaters actually catch fish on such occasions. These claims were systematically dismissed as flights of fancy or inaccurate observations until pellets were found containing fish bones, and in a film featuring Carmine Bee-eaters one bird appears emerging from the water with a fish in its mouth!

[*Merops leschenaulti leschenaulti*, Kotka, Sundarbans, Bangladesh.  
Photo: Gertrud & Helmut Denzau]

The diets and foraging behaviour of most of the *Merops* bee-eaters have been well researched, and those of the sole species in the genus *Meropogon*, the Purple-bearded Bee-eater, seem to be very similar. The spectrum of prey that they exploit is virtually the totality of day-flying insects between the size of fruit-flies (*Drosophila*) and that of strong beetles or hornets up to 40 mm long. Even larger prey are sometimes taken: lacewings up to 70 mm long and dragonflies up to 80 mm long. It is doubtful if any insect flies too fast for a pursuing bee-eater, although the quarry often escapes by taking erratic avoiding action or disappearing into herbage. Only rarely do bee-eaters deliberately discard a warningly coloured, presumably distasteful butterfly; they readily eat blister beetles (*Lytta vesicatoria*), which are highly irritating to human skin, and malodorous bugs, and are undaunted by stinging hymenopterans. Several species actually specialize on stinging honeybees (*Apis*) and bumblebees (*Bombus*) and dangerous wasps and hornets. Inexperienced juveniles apparently prefer black and yellow, wasp-like insects to plain ones.

Bee-eaters hunt almost entirely on the wing, either by making fly-catching sallies from a bare elevated perch or by feeding in continuous flight. Little Bee-eaters are typical of the small, round-winged species. In their preferred habitat of low grass sward interspersed with shrubs, they use perches commanding unobstructed views. A sentinel feeder, the bird constantly surveys the surrounding airspace; on seeing an insect, it dashes after it and either audibly snaps it up only a few metres away or misses and gives up, returning to its perch in a graceful glide. At the perch, the prey item is beaten, stunned, immobilized, and sometimes partly dismembered by being struck against the branch, or its tail is rubbed in order to remove the sting and venom sac. On average, only one foray in three is successful. Prey taking evasive action may be pursued, but chasing flights by Little Bee-eaters seldom exceed 20 m in length or 4 seconds in duration. If a capture is dropped at the perch, the bird dives down and catches it in mid-air in a split second; but, if the insect falls to the ground, it is not retrieved. All bee-eater species are wasteful of insects dropped when adults are attempting to feed young inside

the nest or at the burrow entrance. Many such items are simply too large for the nestling to ingest, and the brood-chamber, the tunnel and the ground below the entrance of cliff nests are often littered with dropped corpses of large insects.

Middle-sized bee-eater species, such as the Red-throated and White-fronted, hunt in bushier and more wooded places, searching for prey from an outer twig 3-5 m above the ground in a leafy tree. So powerful a releaser of pursuit is a flying insect that, when one passes, a perched bird almost invariably makes intention movements, even if it happens to be too satiated actually to give chase. With dashing flight it hawks after an insect up to 15 m away, or sometimes glides slowly towards the ground in order to glean prey in a momentary hover, snapping it up as it rises from herbage. Rarely, both species take an insect from the ground, and exploit swarms of winged ants by catching them in continuous flight aloft.

In open country, the largest, pointed-winged species of *Merops*, namely the Blue-cheeked, Olive, Blue-tailed, European, Carmine, Rainbow and Blue-throated Bee-eaters, forage by fly-catching from a treetop or a telegraph wire. To varying extents, flocks of these species hunt also in easy, wheeling flight on high, catching insect after insect, or so it appears, without coming to perch in between times.

Hymenoptera, comprising bees, wasps, ants and their allies, predominate in bee-eater diets. Of 20 separate studies of 16 *Merops* species, involving nearly one hundred thousand insects recovered from pellets, the overall numerical proportions of Hymenoptera varied from 20% to 96%, with an average of 70%. In part, these high values reflect the abundance and ubiquity of hymenopterans, particularly in the tropics. In addition to feeding opportunistically, bee-eaters seek out and select certain kinds of hymenopterans preferentially from among the aerial insect fauna, choosing such species as honeybees, bumblebees, sweat-bees (*Trigona*) and wasps (*Vespa*, *Polistes*).

A European Bee-eater at the perch typically discerns a bee up to 60 m away, tracks it for an instant, then launches itself abruptly and makes a fast, direct flight to approach the prey





Some bee-eater species are associated with large mammals, usually for the purposes of foraging. In some cases they will use the mammals as static or moving perches, whereas an alternative technique involves following along behind the mammals as they wander through the vegetation.

When the mammals disturb arthropods or small vertebrates, the bee-eaters are swift to pounce on them. This is a technique occasionally used by the White-throated Bee-eater, which will follow not only some of the large African herbivores, but also people and even their vehicles.

[*Merops albicollis*,  
Amboseli National Park,  
Kenya.

Photo: Jacques Gilliéron]



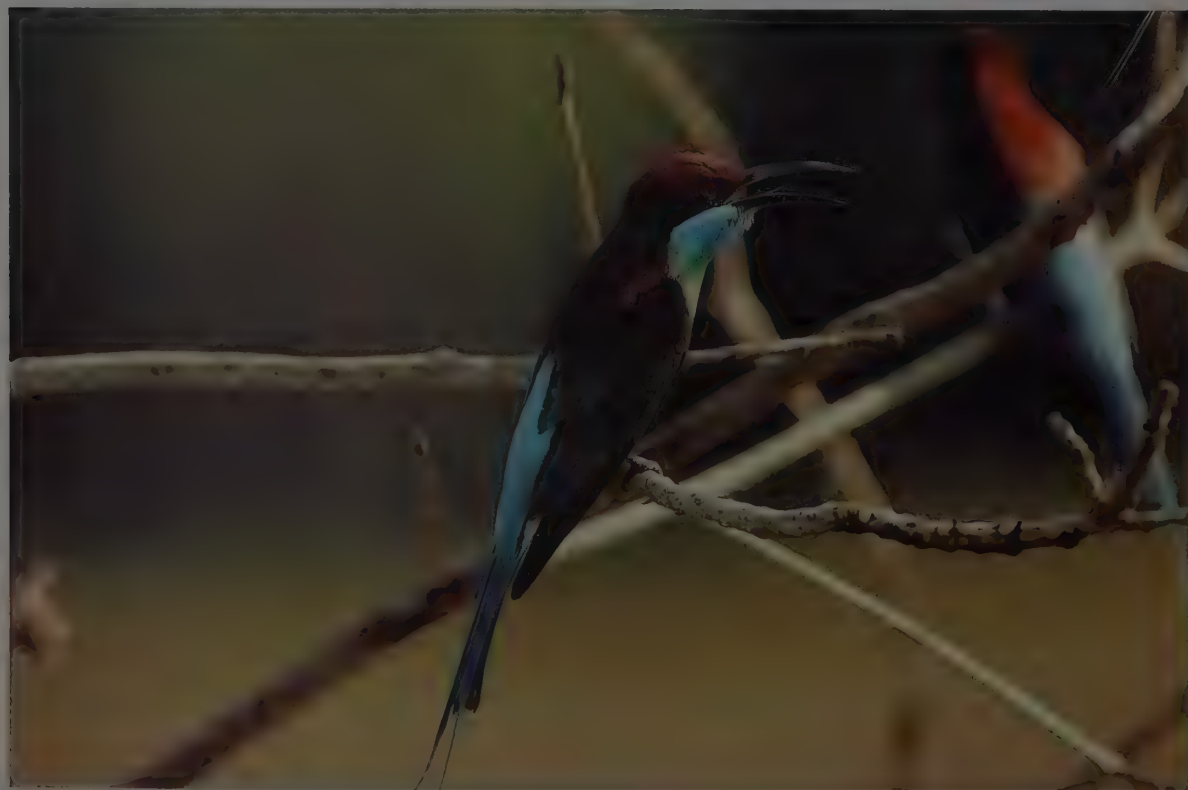
The Carmine Bee-eater is well known for its habit of using other animals as mobile perches. It regularly hitches a lift on the back of Kori Bustards (*Ardeotis kori*), as here; it also rides on Ostriches (*Struthio camelus*) and other large, long-legged birds, as well as a whole host of large mammals. Using its porter as a beater too, the bee-eater takes advantage of prey flushed as the animal advances, in what is essentially a modification involving a mobile sit-and-wait hunting technique.

[*Merops nubicus nubicoides*, Chobe National Park, northern Botswana. Photo: Jacques Gilliéron]

tangentially from behind. Numerous studies have shown that, throughout its range, this species eats mainly Hymenoptera, especially bumblebees, honeybees, wasps of many families, sawflies, ichneumons and ants. Its diet is also made up of beetles (Coleoptera), mayflies (Ephemeroptera), dragonflies and damselflies (Odonata), stoneflies (Plecoptera), grasshoppers, crickets and mole crickets (Orthoptera), earwigs (Dermaptera), mantises (Mantodea), termites (Isoptera), plant-bugs and water-bugs (Hemiptera), cicadas (Cicadidae), scorpion flies (Mecoptera), butterflies and moths (Lepidoptera), caddisflies (Trichoptera) and numerous true flies (Diptera). After Hymenoptera, the largest proportions in diets in most regions are Odonata

and Coleoptera, followed by Orthoptera, Lepidoptera and Diptera. Most prey items are 10-15 mm long. The diets of most other bee-eaters are similar. All species tend to settle socially on the ground for 10-20 minutes in the late afternoon, particularly in the weeks before breeding, and to pick up small fragments in the bill. Grains of sand, bits of snail shell or birds' eggshell, pieces of quartz and even glass cubes from shattered windscreens can be ingested, not as food, but to act as gastroliths or possibly as a calcium supplement.

Because bee-eaters radiate outwards for measurable distances from a favoured perch or the nest to catch individual insect prey, which can often be identified photographically, they make ideal



Most bee-eaters are very vocal birds. Flocks of migrants flying high overhead are readily identifiable as bee-eaters from the rolling, liquid quality of their calls, while the hubbub of a large nesting colony can be heard from far away. All members of the genus *Merops* have rather similar voices, most typically a rather melodious, rolling contact call, which in the case of the Blue-throated Bee-eater, for example, has been transcribed as "terrip-terrip-terrip". Comparatively little is known about the vocalizations of all but a few well-studied species. Contact calls seem to be those most commonly used, while there are also ones related to greeting, appeasement, threat, predator alarm, courtship feeding and the delivery of food by parents to the young.

[*Merops viridis viridis*. Photo: Alain Compost/Bruce Coleman]



Very little is known about the life history of the Somali Bee-eater. This is a small, rather delicate species of arid grassland and scrub with scattered trees and bushes in the region of the Horn of Africa. The diet of the species remains virtually unknown, but its habitual foraging technique involves short sallies from about 3 m up in an Acacia tree in order to catch flying insects. In its very hot environment, somewhat surprisingly it seems quite happy to forage quite busily in the very midst of the midday heat!

[*Merops revuillii*,  
Buffalo Springs Game  
Reserve, Kenya.  
Photo: Luiz Claudio Marigo]



While bee-eaters are acknowledged to be opportunistic feeders, exploiting all available day-flying insects as the occasion offers, at the same time detailed studies have established that Hymenoptera (ants, bees, wasps and allied groups) make up, on average, 70% of their diet. This high figure indicates that bee-eaters are selective, and they do, in fact, show a particular preference for bees.

The Swallow-tailed Bee-eater is certainly no exception; its diet consists almost exclusively of honey bees and, like many of its congeners, it is attracted to apiaries, where it may become a pest.

[*Merops hirundineus*  
*hirundineus*,  
Kalahari Gemsbok  
National Park,  
South Africa.  
Photo: HPH Photography/  
Bruce Coleman]

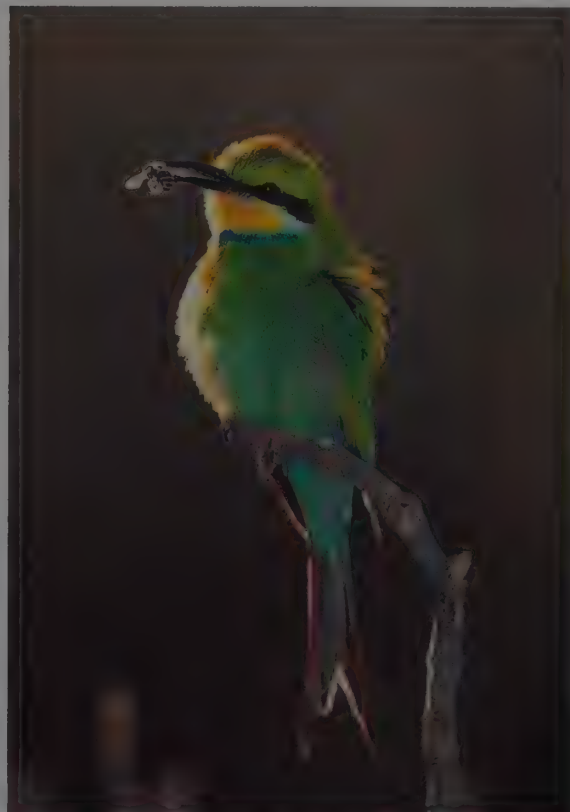
subjects for the study of foraging energetics. For example, in the case of a White-fronted Bee-eater feeding close to its nesting colony, there is no difference in size between prey eaten by the bird itself and prey delivered to its nestlings; the farther away from the colony the adult forages, however, the greater is the size disparity between those small insects which it consumes and the large ones carried back for the young. Nestling White-fronts succoured from feeding territories more than about 3 km away do not grow well, and may die in the nest. European Bee-eaters are able to raise their young on large insects, such as cicadas, caught more than 3 km distant, and on occasion Blue-cheeked Bee-eaters obtain most of their nestlings' food at a distance of 7 km from the nest.

Numerous other bird species, including kookaburras (*Dacelo*) and some swifts (*Hirundapus*), are known to eat stinging bees and wasps, and honey-buzzards (*Pernis*) and honeyguides (*Indicatoridae*) show considerable specialization to that end. Heavy as their toll worldwide may be, however, there is little doubt that the bee-eaters, where they occur, are by far the foremost avian predators of large, stinging hymenopterans, in particular honeybees (*Apis mellifera*, *A. cerana*, *A. florea*, *A. dorsata*). All *Merops* species eat honeybees, and mostly they do so throughout the year and in preference to other hymenopterans. The same 20 studies referred to above revealed the following percentages of honeybees in the diets of the 16 bee-eater species concerned: 0, 2, 3, 5, 16, 17, 20, 20, 25, 25, 25, 45, 47, 50, 52, 54, 67, 80, 83 and 89. Honeybees are hawked wherever they can be found. A breeding European Bee-eater consumes about 39 g of insects per day, or about 410 insects the size of worker honeybees (*A. mellifera*). In Ukraine, a single bird may account for 9000 honeybees during its summer stay. While honeybees comprise only insignificant parts of the diet of bee-eaters inhabiting rainforest and desert edge, they may be eaten practically to the exclusion of all else by resident species in spacious suburban gardens of some African cities, as demonstrated for instance by Swallow-tailed Bee-eaters around Harare, Zimbabwe, and by Cinnamon-chested Bee-eaters around Nairobi, Kenya.

Bee-eaters are well named. It is not surprising to find that the global distributions of *Merops* bee-eaters and *Apis* honeybees are congruent, that is if one takes the range of *Apis* before modern

apiculture made hive bees cosmopolitan. Various bee-eaters have been persecuted by apiculturists because of the inroads that the birds can make into hive stocks.

Only honeybee workers, the sterile females, sting; males or drones do not. Drones are much less abundant than workers, but are two-and-a-half times as heavy. Their size should combine with their being stingless to make them more sought after by bee-eaters.



The rubbing behaviour used to de-venom worker honeybees, as well as wasps and other hymenopteran stingers, is remarkable. Having caught a bee, the bird alights on some firm perch and mandibulates the insect for a moment, grasping it crosswise just behind the thorax. Bending to one side, it deals the bee's head a violent blow against the perch, then it transfers its grip to the tip of the bee's abdomen, bends the other way, and subjects the insect's tail end to five to ten bouts of rapid rubbing. The bill is closed tightly and held side-on to the perch, crushing both abdomen and sting, and the bird, while rubbing, keeps its eyes closed as venom and bowel fluid are discharged and, often, the sting impales itself in the wood. A couple of sharp knocks to the insect's head completes the sequence, which can take up to ten seconds, and the inert bee is tossed back into the throat and swallowed. Whichever way the bee happens to be held, facing either right or left, the direction does not change during treatment, so that all head blows are to one side and all tail rubs to the other. Of the two distinct actions, the rub is used only for stinging (and drone) hymenopterans and the head blow, with variations, for all other insects. Some hard and strong insects may receive up to 80 blows, before they are incapacitated and dismembered sufficiently to be eaten.

A hand-reared Red-throated Bee-eater showed the rudiments of rubbing behaviour the first time it was given a bee to eat, demonstrating that the habit is innate. This particular bird was stung in the mouth by four out of the first five worker honeybees that it ate, which distressed it. Thereafter it was never stung again, and its bee-treatment behaviour improved so rapidly that after only its tenth bee it was practically as adept as adult birds. Bee stings are to be found needling the oesophagus and stomach of adult bee-eaters, which attests to their being stung from time to time. Sixty-five years ago, it was shown that venom of *Apis mellifera* administered at a dose of 0.60 mg per 100 g of body

weight is generally fatal to mammals and small birds. Since a honeybee discharges about 0.2 mg of venom, a 30-g bee-eater surviving a single sting is likely to have some physiological immunity to the poison. Both *Apis cerana* and the large *A. dorsata* are more toxic than *A. mellifera*, and other hymenopterans such as the large, fearsome hornet *Vespa tropica* are, by an order of magnitude, more toxic still.

Ordinarily, a bee-eater captures its prey by flying directly at it and seizing it with the bill pointing forwards along the flightpath. Blue-cheeked and Blue-tailed Bee-eaters have a unique method of catching large and dangerous stingers, although it has been observed only four times. A perched Blue-cheeked Bee-eater in Nigeria repeatedly flew out after large sphecids wasps up to 100 m away; closing on one from below, it threw its head back with the bill pointing vertically upwards, seized a wasp in the very tip of the bill, nibbled it for several seconds, tossed it up in mid-air and then chewed it again. Blue-tails in Malaysia behaved in much the same way, scanning from high-tension cables across a chequerwork of square paddyfields, discerning an insect 80-95 m away, flying out fast and level, passing immediately below it and, at the last moment, reaching up with the bill pointing vertically or even behind the vertical; this extraordinary posture was retained for a full second after the hornet had been seized. Blue-tailed Bee-eaters foraging from trees bordering an estuary flew from 10 m to 70 m out over the water to intercept large hornets (*Vespa tropica*), seizing each from below in the bill tip, and maintaining the skyward-pointing posture while making the first few wingbeats for the return to the trees, where the prey was beaten and rubbed. On another occasion, Blue-tails were feeding on giant honeybees (*Apis dorsata*) flying low over a games field, and what was then remarkable was that the birds attacked the insects from below with the sky-pointing posture momentarily sustained, when the insect



Much research into the European Bee-eater's diet has revealed that it feeds chiefly on Hymenoptera species, with beetles and dragonflies amongst the groups of secondary importance. In fact, it will avail itself of any flying insects, provided they are the right size, roughly 5-50 mm long. It regularly exploits a single food source for a long spell, if the prey is found in abundance, as, for example, occurs with locusts and termites. It is capable of spotting prey 50-100 m away and launches itself from its perch in pursuit, a sometimes lengthy chase ensuing before the insect is captured and taken back to the perch to be devoured. It also hunts high in the sky, where small insects are devoured on the wing.

[*Merops apiaster*,  
Dueñas, Palencia, Spain.  
Photo: Juan Martín Simón]



In its handsome plumage of blue, russet and black, the Blue-headed Bee-eater is one of the lesser known and more secretive Merops species. It breeds in a discontinuous line across the African rainforest zone from Sierra Leone to eastern Zaire, with a small isolated population in Kenya.

A small, rather silent bird it inhabits lowland forest. Like most sedentary bee-eaters with rounded wings it likes to hunt from an exposed perch within 4 m of the ground, making short sorties after passing insects. Its main food is bees, but it also takes a wide range of other insects, including butterflies and moths, as here. The sharp points of a bee-eater's bill are not used to stab at and impale insects, but rather the two edges serve as forceps, enabling the bird to pluck insects out of the sky; it seizes them in the very tips of the bill, where they are crushed and often devoured in flight. Large items are invariably taken back to a perch, one by one, and dismembered by beating. In the case of bees, their tails are rubbed against the perch to get rid of the sting and venom. So deft and lightning-quick are their movements that bee-eaters are rarely seen to drop an insect. If that should happen, the bird is usually adroit enough to catch it before it reaches the ground!

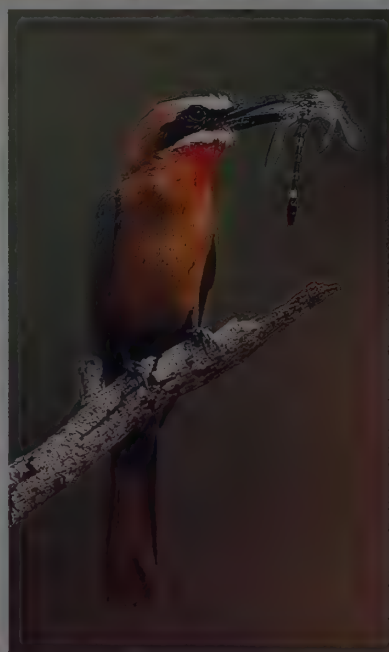
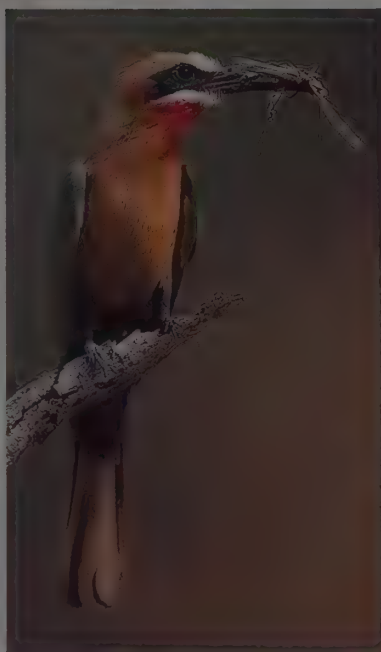
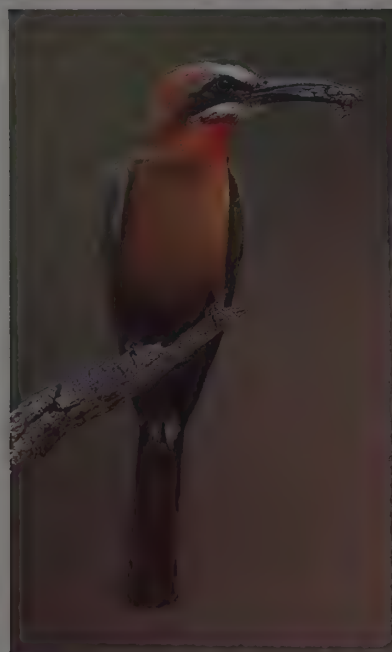


[*Merops muelleri muelleri*,  
Kenya.  
Photo: Michael McKavett/  
Bruce Coleman]



True to their common name, bee-eaters do indeed feed principally on bees, as well as other allied Hymenoptera. In some species the proportion may be as high as 96%, although in others, a minority, it can be as low as 20%. As these White-fronted Bee-eaters show, many other types of prey are also taken, and it has been established that the main constituents of their diet may vary considerably in accordance with season and availability. The universal bee-eater habit of regularly regurgitating pellets has enabled scientists to prove, by careful analyses, that bee-eaters exploit nearly all the day-flying insects that occur in their respective habitats; only those that are too large or too small are ignored.

[Above: *Merops bullockoides*, Linyanti Reserve, Botswana.  
Photo: Daryl Balfour/NHPA.



Below: *Merops bullockoides*, Zimbabwe.  
Photos: Mike Wilkes/Aquila]

itself was only half a metre above the turf. Incidentally, the Nigerian observation, by M. Dyer in 1980, remains the only one of any bee-eater species eating stingers without returning to a perch to remove the sting. A Blue-cheeked Bee-eater caught two or three more wasps in succession, dealing with the first ones while flying, and returning to its perch with the last one to dispatch it in the usual manner, by beating and rubbing.

White-throated Bee-eaters are small and rather round-winged, yet on their wintering grounds they spend much time high above the forest canopy, evidently feeding in continuous flight. In winter, they subsist largely on ants, and doubtless exploit these insects swarming above the forest: the prey are presumably crushed by a snap of the bill and swallowed forthwith.

Both northern and southern subspecies of the Carmine Bee-eater are strongly attracted to bush fires. The birds appear excited, perching on charred shrubs and dashing about the flames and through the smoke to catch fleeing insects, generally locusts and grasshoppers. Another strong foraging association of Car-

mine Bee-eaters is with large mammals and birds and with vehicles. White-throated and European Bee-eaters occasionally follow behind people and vehicles moving through the African bush, catching insects disturbed from the grass. Carmine do the same, but far more regularly, although their main stratagem is to feed in effortless sailing flight, straight or in wide circles, flapping for only a tenth of the time. They forage at heights of about 50-100 m in bouts of five or ten minutes, alternating with rather longer resting periods at a perch; they often soar falcon-like, rising on thermals. A quick acceleration with wings flailing, ending in a sudden swerve or swoop, must denote the capture of prey. There is circumstantial evidence that Carmine Bee-eaters sometimes eat honeybees on the wing without returning with the prey to a perch, but this will be difficult to prove.

A single Carmine Bee-eater was watched one day for seven-and-a-half hours. It spent over two hours feeding high in the air and made 100 dashes in pursuit of prey. For the rest of the time it perched on trees, and made 40 or so fly-catching sorties.



Much bee-eater foraging is carried out from an exposed perch. The bee-eater darts off, much like a flycatcher, in pursuit of a passing insect, usually returning with it, once captured, to the perch, where it is suitably "processed". Most items are first immobilized. Holding a wood-wasp firmly in the tips of its bill, this Carmine Bee-eater twists its head almost upside-down, and beats the wasp against the branch until resistance ceases, and the prey can be swallowed comfortably. All stinging species are devenomed: the tail end of the insect undergoes 5-10 bouts of rapid rubbing to provoke the discharge of both sting and venom. Soft-bodied prey like moths may be eaten without beating, but tougher insects are subjected to a prolonged beating session before being deemed sufficiently tender for consumption.

[*Merops nubicus nubicoides*,  
Kruger National Park,  
South Africa.  
Photo: Rolf Kunz]



Northern Carmine Bee-eaters commonly, and southern Carmines uncommonly, sit on the highest point of the back of walking Ostriches (*Struthio camelus*), Kori Bustards (*Ardeotis kori*), Arabian Bustards (*A. arabs*) and grazing sheep and goats, using them as beaters to disturb insects. They also use storks (Ciconiidae), herons (Ardeidae), ibises (Threskiornithidae), cranes (Gruidae), Secretarybirds (*Sagittarius serpentarius*), cattle, camels, donkeys, zebras, antelopes and warthogs (*Phacochoerus africanus*) as animate perches. Confiding birds, they fly slowly behind or swoop around a person, snapping up small insects rising from the vegetation. They fly alongside a galloping beisa oryx (*Oryx beisa*) at shoulder height, or several metres behind it; and they fly alongside cars, trucks and tractors, keeping station except to swoop down now and then for an insect, and sometimes they even ride on the vehicle.

This bee-eater species forages opportunistically, and at times an individual will feed exclusively on a single swarming prey species. Some pellet samples have been found to consist almost

entirely of honeybees, and others of chafers, winged ants, shield-bugs (*Coridius viduatus*), cicadas (*Ioba leopardina*; fed to nestlings when the adults were themselves feeding on termites) or locusts (*Locusta migratoria*). In the Niger River Inundation zone in Mali, locusts seem to be this bee-eater's staple. Recognition of that region as a major hatching ground of migratory locusts promoted studies of their predators, among which Carmine Bee-eaters featured importantly. From January to May, locusts move north-eastwards down the Niger floodplain, following the falling waters and breeding as they migrate; the bee-eaters exploit these insects, evidently migrating with them, and feeding also on desert locusts (*Schistocerca gregaria*) and at least ten other locust and grasshopper genera.

Northern Carmine Bee-eaters may be in the process of diversifying their hymenopteran diet with incipient specialization upon locusts. Similarly, Blue-cheeked Bee-eaters are dragonfly specialists and Böhm's Bee-eater relies to a large extent on flies. Ants form a major component in the diets of the Little Green,



White-throated, Rosy and Carmine Bee-eaters. European Bee-eaters in Africa eat mainly winged ants and termites, but in Europe their staple is the bumblebee.

White-throated Bee-eaters breed along the southern borders of the Sahara, but spend the non-breeding season in woody savanna and around rainforest. In each region, they have exceptional feeding strategies. In the desert, they supplement their diet

of airborne insects with lizards up to 40 mm long; or at least they feed the latter to their nestlings, even if they do not eat them themselves. On their wintering grounds, where oil palms (*Elaeis guineensis*) are abundant, there is an extraordinary relationship with squirrels (mainly *Funisciurus anerythrus*) and weavers (including *Ploceus cucullatus* and *P. castaneofuscus*). Squirrels and weavers regularly eat the oily and highly nutritious mesocarp of oil palm nuts. A squirrel in the head of the palm plucks a nut, holds it at both ends, tears off and discards in strips the fibrous, oily outer layer, and gnaws the succulent flesh. At the height of the dry season, when airborne insects are scarce, the bee-eaters forsake their usual diet with alacrity and attend upon any squirrel they find in an oil palm. Up to ten bee-eaters gather in the fronds below the squirrel, some within 40 cm of it, and intercept the strips the instant they are dropped below a frond. Some strips are not taken in the air, because they lodge in the frond bases at the squirrel's feet, where weavers grab them. The bee-eaters sometimes fly at the weavers, strike them with their wings, and catch in mid-air any strips that the weavers drop. They sometimes attend upon weavers after the squirrel has departed.

Other instances of bee-eaters consuming vegetable matter have been recorded. Once, many European Bee-eaters died in cold weather in Zimbabwe, and some of them had hard green berries of a shrub (*Cedrela toona*) stuck in the throat. A further example concerns loafing Carmine Bee-eaters in Botswana which picked up and, curiously, ate large seeds of the poison-pod *albizia* (*Albizia versicolor*).

Bee-eaters of several species have been found to eat flightless prey. Spiders and caterpillars sometimes occur in pellets; although wingless, they may have been airborne, since they spin threads of silk by which to hang below herbage or to disperse on the wind. A European Bee-eater has been seen trailing a long silken thread. Harvestmen (Opiliones), woodlice, flightless ground beetles, flightless driver-ant (*Dorylus*) soldiers, and grubs also occur in pellets, and on rare occasions a bee-eater will take a small insect from herbage, and will even consume earthworms.

Most bee-eaters occasionally splash down on to the surface of still water, and may even immerse themselves entirely. This

Once an insect has been battered and, if applicable, its sting removed, it is tossed in the air and swallowed, in a swift, co-ordinated movement, as demonstrated by one of these Cinnamon-chested Bee-eaters. This species is a typical sit-and-wait hunter, perching on an exposed site, and sallying forth to catch passing insects. Honeybees (*Apis mellifera*) make up the vast majority of its diet. Other, better-studied bee-eater species have been found to take some 410 bees per day, and some 9000 over the breeding season.

[*Merops oreobates*, Masai Mara National Park, Kenya.

Photo: Günter Ziesler]

Scientists researching the diet of bee-eaters are greatly aided by their convenient habit of regurgitating pellets containing the indigestible remains of their insect prey, as seen here in a European Bee-eater. The fresh pellet is black, odourless, and on average 1-3 cm long. Nestlings begin by producing one pellet per day; then from ten-days-old they cough up two. The frequency of regurgitation in adults is a pellet every one and a half to four hours, depending on the kind of prey taken more than on the quantity.

[*Merops apiaster*, Lesbos, Greece. Photo: Mike Wilkes/Aquila]





behaviour has often been interpreted as diving for aquatic insects, although most observations probably refer to bathing, especially when the action is followed by a bout of preening. The fact is, however, that at least three species do eat fish, however rarely. In Africa, pellets found on the shores of Lake Victoria, probably deposited there by Blue-breasted Bee-eaters, contained scales thought to be of a cichlid 30 mm long that feeds in the surface film, while pellets known to have come from Blue-tailed Bee-eaters feeding along a shallow stream in Malaysia contained bones of 35-mm poeciliid fishes (*Gambusia affinis*). Moreover, a Carmine Bee-eater in Zambia has been captured on film, splashing tern-like on to a river surface and rising one-fifth of a second later with a fish about 5 cm long held crosswise in its bill. Kingfishers sometimes catch bees, and it is an interesting thought that bee-eaters sometimes take fish.

### Breeding

All bee-eaters are earth-hole nesters, excavating their own tunnels, with an oval egg-chamber at the end, starting in level ground or an earthen cliff face. They lay a single clutch annually, larger at high latitudes than in equatorial ones, and nearly always dig a fresh burrow each year. Sometimes they refurbish the previous year's nest, or very rarely use a suitable rodent burrow. Bee-eaters are quite long-lived, but at least the migratory species tend to pair up anew each breeding season. Pair-bonding, courtship and pre-copulatory behaviour are not spectacular; indeed, for some species they have barely evoked any remark at all. Among the Meropidae, these aspects of breeding are in large part vocal, accentuated with lifting of the crown and throat feathers, spreading and quivering of the tail, and momentary wing-raising. Courtship feeding is widespread across the family. White-throated Bee-eaters have a "butterflying" display, a high-winged glide alternating with shallow wingbeats, accompanied by vociferous calling. The male and female perch facing each other with wings raised high, then fold the wings, raise the crest feathers into a peak, bob up and down by rapidly flexing and extending the legs



and then, as a prelude to copulation, move the beak on the perch as if de-stinging a bee by rubbing its tail.

Smaller or forest-dwelling bee-eaters are generally short-winged and sedentary, nest solitarily, and live all year in a home range that is a feeding territory and includes the nest. Middle-

Bee-eaters are not noted for spectacular courtship behaviour, perhaps least of all the *Nyctornis* species, but here a Blue-bearded Bee-eater, in the company of its mate, has adopted a rather stylized stance. Little is known about the courtship of this species, but it seems to have some sort of food-offering display, which involves one bird flying onto a perch alongside its partner, after which both individuals fan their tails and go through a series of stereotyped bows.

[*Nyctornis athertoni* athertoni,  
Khao Yai National Park,  
Thailand.  
Photo: Arnoud B.  
van den Berg]

One of the most frequently observed interactions in bee-eaters is courtship feeding, when a female is fed by her mate, or in some colonial species also by male helpers. This Little Green Bee-eater accepts the proffered food item, which is not necessarily always a large succulent one. The act is often followed by copulation, after or even before the female has had time to swallow the offering. More rarely the male mounts her without surrendering the courtship feed and, when copulation is over, he eats the insect himself!

[*Merops orientalis*  
*cyanophrys*,  
Israel.

Photo: David Cottridge/  
BBC Natural History Unit]





Courtship feeding is observed in the European Bee-eater soon after the birds arrive on their breeding grounds, already paired from their wintering quarters in Africa. With his perched mate looking on, the male catches an insect and alights beside her, facing the same way and calling at the same time, despite his full bill. Then he stretches forward, offering the prey. The female usually accepts the gift and swallows it. She then adopts a soliciting posture, by lying almost horizontally on the branch, with head and throat feathers ruffled. The ensuing copulation lasts up to 10 seconds. Courtship feeding may take place as many as eight times before mating occurs. Non-breeding birds, usually adult males, sometimes attach themselves to a breeding pair and act as helpers. They will also feed the female, though their attempts to mate are normally repulsed.

[*Merops apiaster*, Neusiedler See, Austria. Photo: Manfred Pfefferle]

sized species breed in small, often compact colonies, while large, long-winged, woodland, grassland and desert-edge bee-eaters are mostly migratory, travel several kilometres each day in search of food, and nest in huge aggregations of from hundreds to tens of thousands of birds. Most or all of the colonial species have adult helpers at many nests, and there is no doubt that the survival of a brood of young is enhanced when it is reared by multiple adults, rather than by just the two parents. Many nest-holes come to grief, and, even if they do not, half of the brood often starves to death when poor weather deters insect prey from flying. All bee-eaters have an interesting stratagem for tailoring the number of survivors in a brood to the supply of food. There are generally about five eggs in a clutch, laid on successive days, and incubation begins with the first eggs laid. The eggs therefore hatch at daily intervals, and the sizes of the chicks in the brood are accordingly staggered. Insects are brought into the nest one at a time, and the largest, most aggressive youngsters get the lion's share. In a good year with plentiful food, and particularly if the parents have helpers, even the latest-born, smallest member of the brood has ample sustenance and it survives to fledge healthily. Otherwise, a cut-off point applies itself somewhere in the size hierarchy, and the weaklings go under.

A compact, sandy or loamy soil is sought for the nest, though the bee-eater's sharp bill and free use of both sharp-clawed feet in excavation means that even hard clays and laterites can be used. Red-throated and, sometimes, Carmine Bee-eaters excavate their nest-burrows three or four months in advance of egg-laying, when the earth is still easily penetrable at the end of the rainy season. The softer the ground, the longer tends to be the burrow, within limits characteristic of each species. Burrows take a week or more to dig, and the bird's bill becomes worn and shortens by about 2 mm. Many burrows are abandoned when only half excavated, and are replaced by a full-length one dug nearby.

There is a balance of advantages and disadvantages between nesting in level ground and nesting in cliffs. Burrows in flat

ground are more prone to be raided by small predatory mammals, snakes, lizards and rodents. They are sometimes flooded out, and are highly vulnerable to trampling by cattle, buffaloes or elephants. On one occasion, an entire sand-dune colony of nesting White-throated Bee-eaters was immured under blown sand and entirely obliterated, adults and nestlings alike. Nests in cliffs are usually dug into the top half of the face, freeing them from the attentions of most ground predators. They are better protected from rain, but are parasitized by honeyguides. Spitting cobras (*Naja nigricollis*) and egg-eating snakes (*Dasypeltis scaber*) often raid nests in Africa by reaching down from the cliff top: a large monitor or goanna lizard (*Varanus*) is quite capable of digging a gaping hole to eat several broods; and African Harrier-hawks (*Polyboroides typus*) try to grab the odd nestling that ventures too near to its cliff-burrow entrance. When disaster does strike a cliff-nesting colony, it can do so on the grand scale. Colonies are often in riverbanks, and can be inundated by a flash flood; worse still, the entire cliff face is often so undercut by the stream, or so riddled with nest-holes, that it collapses, destroying all eggs and young and many adults, thereby nullifying an entire year's production of offspring.

Cinnamon-chested, Red-throated and White-fronted Bee-eaters nest only in cliffs, usually at least 2 m high. Their tunnels invariably slope steeply upwards for 50 cm, which keeps out the rain, then angle over a hump in the floor down into the egg-chamber, which helps to save eggs and hatchlings, but not larger young, from falling out. Other species are more versatile and dig their nest-holes in high cliffs or low slopes, or in quite flat ground. The densely packed nests of Carmine Bee-eaters sometimes spread up over the cliff top on to level ground, while Rosy Bee-eaters site their huge colonies on sandbars exposed by falling waters of the great West African rivers. A nesting site favoured by the Little Bee-eater is the sloping roof just within the entrance of the deep lair of an aardvark, perhaps the safest site of all.



The Blue-cheeked Bee-eater is monogamous, and may pair for life; certainly, throughout the year, pair members associate more with one another than with other flock members. As part of pair-bonding, the birds may wrestle with their bills locked; they also display with the wings raised at the carpal joint and the coppery undersurface on show. Preceded by a courtship-feeding ceremony or initiated by a soliciting call from the female, at a spot defended by the pair, mating takes place on a perch or on the ground. If on a perch, the male approaches his mate by side-stepping, before he mounts her, usually gripping feathers on the female's head in his bill as they copulate. If the female is stretched across the perch, he must perform no mean acrobatic feat to maintain his balance, and only manages not to topple backwards by holding the wings spread wide and high above him and bearing down with the bill against his mate's forehead. On the ground the whole operation looks less hazardous and infinitely more dignified! The female crouches low, in submissive posture and with her tail held sideways, while the male half-supports himself on his tail which he rests stiffly on the ground behind him. In the European Bee-eater (*Merops apiaster*), which shows similar sexual behaviour, the frequency of copulation may increase to up to 10 times a day until the clutch has been completed, when all mating ceases.

[Above: *Merops persicus persicus*,  
Hafeet, Oman.  
Photo: Hanne & Jens  
Eriksen/Aquila.

Below: *Merops persicus persicus*,  
Abu Bagra, Oman.  
Photo: Hanne & Jens  
Eriksen]





All bee-eaters make their nests in holes in the earth, almost invariably dug afresh each year. The type of site chosen varies widely with species and even within species. The Blue-tailed Bee-eater prefers the dry sandy banks of waterways, but will also nest in coastal dunes or flat grassy ground, and at times even in sea-cliffs. Both sexes participate in the excavation work which may involve a series of "false starts". The final burrow with its terminal nest-chamber, may be as much as 2 m long, and take up to 20 days to complete.

[*Merops philippinus*, Sundarbans, Bangladesh. Photo: Gertrud & Helmut Denzau]

European Bee-eaters are summer breeders, and they pair up on their African wintering grounds. The main arrivals of this species in east Arabia are in mid-March, in south-west Europe two weeks later, and in Central Asia in mid-April, and everywhere in the Palearctic egg-laying takes place around May. The Blue-cheeked Bee-eater lays two or three weeks later. European Bee-eaters can breed in their first year. The males tend to return to their natal colony, but young females tend to disperse distantly. In Russia, at least 80% of birds return to the site of their previous year's colony. Here, males are said to select the nest-site, taking about three days. The pair, with any helper, starts digging two or three holes at once, soon abandoning the "false starts". They can dig nearly 40 cm of tunnel a day, although it usually requires ten to 20 days to complete the burrow, 1-3 m long, and the brood-chamber at its end. A clutch of seven eggs takes one week to lay, and each egg takes 20 days to incubate; incubation begins with the first or second egg, and is by both or all birds by day and by the female alone at night. The eggs are subspherical and lustrous white, fine-grained and porcelain-like; the shell is thin, and new-laid eggs look pink with transmitted light, but they soon become dull, opaque white. Hatching takes from two to six days, and the nestling period is about 30 days, the whole brood leaving the nest on the same day or on two successive days. In South Africa, European Bee-eaters breed six months out of phase with those in Europe and Asia.

The length of time from the start of egg-laying to the young European Bee-eater leaving the nest is thus about eight weeks. For small, tropical species, the corresponding period is six to seven weeks. In the northern tropics, nearly all bee-eaters are summer or wet-season nesters, rearing their young in the two or three months when insect food is most abundant. At latitudes in West Africa where the annual rains are ephemeral, the various bee-eater species all nest at about the same time. Where the rains last for several months, however, the half-dozen species stagger the start of breeding over a period of six weeks or more, which may have the effect of reducing interspecific competition for re-

sources; the earliest nester there is the Red-throated Bee-eater, which for ill-understood reasons breeds in the late dry season. In southern Australia, Rainbow Bee-eaters breed in November to January, whereas in the north they nest before or after the long wet season, generally about September-October and May-July. South of the equator in Africa, bee-eaters are also summer breeders: for instance, European Bee-eaters nest in South Africa in September-January.

All bee-eaters hatch naked, blind and pink, and have dry, wrinkled skin, drooping wings, a swollen belly, and the lower mandible slightly longer than the upper. For some hours the head is too heavy to be held up; the body is supported on the belly and the tibiotarsal joints. By the fifth day, the skin has become shiny and the eyes begin to open; the belly can be raised off the ground, and the bird can move forwards and backwards with a shuffling but rapid gait. During its second week the young bird looks like a hedgehog, being covered with pointed grey spines. Soon the feathers break through, and it acquires plumage much like that of the adult, although the parts that are chestnut on the adult may be green and the reds pale pink. Nestlings are quarrelsome, and one hogging the inner end of the tunnel as it waits for a parent to come in with food can be tugged by its tail until it yields its place to a hungrier sibling. A well-grown nestling can be up to 20% heavier than the adult, but its weight falls in the few days before it leaves the nest, by which time it is only a gram or two above the parental weight. For the first day or two out of the nest the young bee-eaters do not catch their own food. Adults feed them decreasingly until, at two or three weeks, the juveniles are entirely independent.

African Red-throated Bee-eaters north of the equator and White-fronted Bee-eaters south of it nest in cliffs in dense colonies with up to 200 burrows, although five to 50 is the usual number. At least in larger colonies, the majority of male-female pairs of mated birds are helped in most duties by another adult (indistinguishable to human eyes, though all birds in a colony recognize each other individually) or occasionally by up to five





European Bee-eaters nest in holes which they excavate in vertical banks, sloping ground or, as here, fairly level ground.

First of all, the birds will glide around over a prospective site for about three days, apparently making up their minds on the precise location to be occupied. Eventually, one bird, thought normally to be the male, starts digging and thus effectively selects the definitive site; both birds then share the digging duties. At a level site, the hole is started by the bird scraping with its feet. Then, as the depression deepens, the bird uses its sharp, pointed bill as a pick to dislodge the soil, and, supporting itself on bill and carpal joints, scrabbles the loosened particles backwards with both feet. If a European Bee-eater runs across pebbles or tough clods, it will carry them out of the nest in its bill, and in one case birds were recorded tunnelling right through a root which obstructed their progress! During the 10-20 days or so of excavation, the bill becomes blunted, and tends to end up some 2 mm shorter.

[*Merops apiaster*,  
Embalse de Rosarito,  
Toledo, Spain.  
Photos: Jorge Sierra]





The Blue-bearded Bee-eater makes its nest-hole in sandy banks by streams or alongside paths cut through the forest; other sites chosen include road cuttings or steep cliff faces in forested ravines. Although it nests in solitary pairs, as many as 20 unfinished holes may pepper the same site, giving the impression of a full-scale colony. Excavation work begins as much as a month before the eggs are laid and the definitive burrow, measuring up to 3 m in length, widens at the end into a nest-chamber some 13 cm high. Nests are unlined, but rapidly fill with pellets, since both adults roost there before and during egg-laying and incubation.

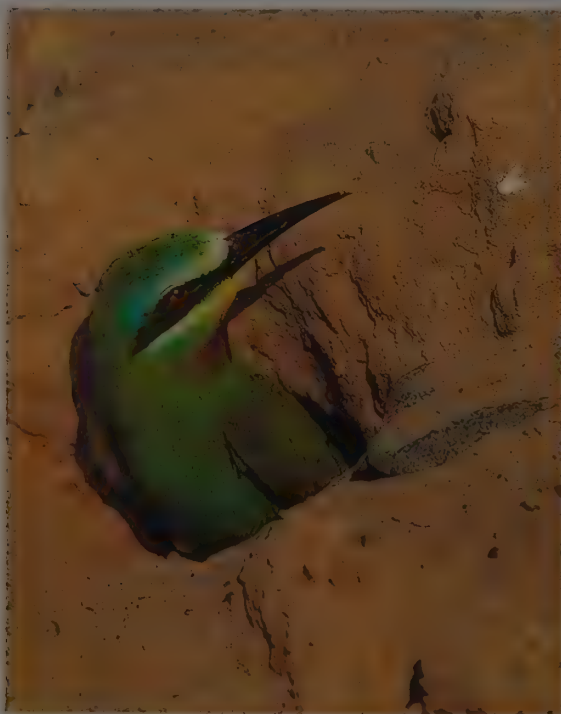
[*Nyctyornis athertoni athertoni*, Khao Yai National Park, Thailand.  
Photo: Arnoud B. van den Berg]

other adults, mainly males and mostly the previous year's offspring of the pair being helped. Three or four pairs with their helpers comprise a clan, so that a large colony may have some three to six clans. The nest-burrow entrances of one clan are not necessarily adjacent on the cliff face, as a clan's nests are scattered through the colony. Clan-members freely visit each other's

nests, not just sitting at the entrances but entering the brood-chambers, but birds in the colony which are not members of the particular clan are chased away from the clan's nest-holes. The birds are long-lived and sexually opportunistic, even if pairs are essentially monogamous, and, as with humans, strands in the web of social complexity are constantly shifting.

The assertion that bee-eaters recognize some, and probably all, individuals in a colony of hundreds arises partly from the demonstration of individual differences in and recognition of voice, as demonstrated in the 1990's by C. M. Lessells and others, and partly from demographic studies. S. T. Emlen and colleagues have spent thousands of hours in studying the fortunes of particular colonies of White-fronted Bee-eaters over many years, and it is amply clear that an individual bird knows and remembers its parents, siblings, offspring, friends and nesting neighbours.

Six species of bee-eater always nest solitarily. These are the Red-bearded, Blue-bearded, Purple-bearded, Blue-headed, Little and Blue-breasted Bee-eaters. Seven nest solitarily or in small, loose colonies. Cinnamon-chested and Rainbow Bee-eaters usually form loose colonies. Six species breed in colonies that vary from loose to dense, and with a few nests to many hundreds. The final four breed in compact colonies, Red-throated and White-fronted with tens or hundreds of nests, Carmine with hundreds or thousands, and Rosy Bee-eaters with tens of thousands. That forest species are solitary is thought to relate to the fact that insect resources in such habitats are evenly distributed and their populations constantly replenish themselves. The Little Bee-eater, in grassy woodland, has a nesting territory large enough to ensure a regular supply of small insects, but not so large that the pair cannot defend it. At the other extreme, the large and long-winged Carmine and Rosy Bee-eaters must fly far and wide every day to find sufficient bees or a hatch of good-sized high-flying bugs. When feeding grounds are necessarily distant, they cannot be defended by a nesting pair against other individuals, and there are survival advantages in the alternative



A Blue-cheeked Bee-eater emerges from its nesting hole dug in hard sloping sandy ground. It nests most frequently in loose colonies, often sharing a site with European Bee-eaters (*Merops apiaster*). Tunnels vary considerably in length: generally speaking the softer the earth, the longer the tunnel. In banks or cliffs, the tunnel is nearly straight and horizontal, whereas in more level ground it declines at about 20%, ending in a nesting chamber.

[*Merops persicus persicus*, Abu Baqra, Oman.  
Photo: Hanne & Jens Eriksen]



stratagem of breeding coloniality. Following a ten-year study during 1985-1994, S. M. Kossenko and C. H. Fry have recently suggested that European and Blue-cheeked Bee-eaters in Asia may in fact prove to breed more successfully in mixed colonies than in monospecific ones; the two species seem not to compete for nest-sites and often nest quite separately, but in mixed colonies they co-exist perhaps by trading off food competition against improved breeding success.

### Movements

Tropical forest bee-eaters are sedentary, and small, tropical open-country ones are more or less sedentary, too. Within Africa, several species are migratory, most notably the White-throated, the Carmine and the European. White-throated Bee-eaters breed in May-September in a narrow belt from Mauritania across to Eritrea and Yemen, and thence southwards through Djibouti to the Kenyan Rift Valley and Mount Kilimanjaro, being resident in the last area. From the borders of the Sahara, however, they migrate into the coastal and equatorial forest belt, travelling by day with considerable regularity, in loose flocks that forage as they move. Wintering birds at the mouth of the Congo River are 2200 km from the species' nearest breeding region, at Lake Chad, but would have to travel 3000 km if they nest in, say, Sudan. There have been no ringing studies to ascertain their exact destinations. Just before departure from southern Nigeria they lay down migratory fat, increasing their weight by up to 15%. In spring, migrants occur at Cape Guardafui in northern Somalia, although it is not known whether they cross the Gulf of Aden to east Yemen or loop westwards to make the much shorter crossing of Bab el Mandab between Djibouti and west Yemen. Even overland flights can be a danger, for in some years hundreds of White-throated Bee-eaters arriving in April at their breeding grounds in Mali perish in sandstorms.

At least the southern subspecies *nubicoides* of the Carmine Bee-eater has an unusual tripartite migration. It breeds in September-November in a zone from Cunene, in Angola, and the valleys of the Chobe, Zambezi and Luangwa, south to 21° S in Zimbabwe and Mozambique. After breeding, it moves south into Namibia, Botswana and well south of the Limpopo, as far as Richard's Bay, in Natal, withdrawing by March and traversing the breeding grounds to spend the next six months, from March to August, on the main non-breeding grounds, mesic savanna from northern Angola, Kasai Oriental, Kivu, Burundi and north-west Tanzania south to 15° S.

European Bee-eaters from the Mediterranean and the south-west and central parts of Asia spend the non-breeding months in West Africa and in the eastern half of southern Africa. Quite a separate population, numbering about 20,000 birds, breeds in October-December in the western half of South Africa and in south Namibia. R. K. Brooke and P. Herroelen (1988) have shown that this latter, western, population spends the non-breeding season, the austral winter, within Africa, in a vast region from Transvaal to Malawi and north-west to a line from Bengo, in Angola, across to Lake Victoria.

The same species is a summer visitor to its northern temperate breeding grounds, where it ranges from north-west Africa and Europe east to Oman, north Pakistan and east Kazakhstan. European Bee-eaters nest north to approximately the 21°C July isotherm, in places at 53° N and 55° N, and they winter almost entirely in Africa. They generally migrate by day, often flying high in loose, calling flocks of 20-40 individuals that are thought to include family parties. They cross deserts and seas on a broad front, although they also follow rivers and coastlines and concentrate along the Black Sea coast and at Gibraltar. Migrants crossing the Sahara are compelled to travel by night as well as by day, and nocturnal movements occur quite widely elsewhere. Migratory flights are punctuated by feeding, the birds hunting aloft or coming down to perch. The deposition of migratory fat

As male and female look alike in nearly all the bee-eater species, ascertaining the roles played by each sex is somewhat difficult.

The male is thought to select the nesting site and both pair members take turns at excavating the tunnel. At least in some species the adults share incubation, taking alternating daytime shifts; at night only the female sits. In most bee-eaters it is usual for both parents to feed the nestlings. The Black-headed Bee-eater, an African rainforest species, nests solitarily or in loose colonies, breeding in pairs but often with a third adult in attendance. The helper is not known to incubate, though it may participate in tunnelling; its principal function seemingly is to assist in feeding the young.

[*Merops breweri*, south-east Nigeria. Photo: C. H. Fry]







Colonial cliff nesters have certain advantages. Though not immune from predation by small mammals, snakes, lizards and rodents, they are certainly less open to it, and are also better protected from the rains. In addition, the presence of many eyes helps in detecting potential predators, above all aerial ones, and the colony acts as an information centre, enabling all its members to exploit any freshly discovered source of food. On the other hand, colonies in riverbanks may be swamped by flash floods or even worse become so undercut that finally the whole cliff collapses, wiping out the whole colony. The Carmine Bee-eater is one species that always breeds in spectacular dense colonies, consisting of hundreds or frequently thousands of birds. Most are located in cliffs above large rivers, often in association with smaller ones of Red-throated (*Merops bulocki*), or White-fronted Bee-eaters (*Merops bullockoides*). The colony may occupy the same site for decades, sometimes overflowing into the level ground behind; others shift a few hundred metres each year. Some of the best known and most accessible colonies have become great tourist attractions, especially for photographers and ornithologists. However, the birds are liable to desert a colony, if subjected to too much human interference. It is estimated that the known colonies represent only a fraction of those actually in existence, and that consequently the total population of Carmines could run into millions.

[Above: *Merops nubicus nubicoides*, Matusadona National Park, Zimbabwe. Photo: Jeremy Woodhouse/DRK.]



Below: *Merops nubicus nubicus*, north Cameroon. Photo: Michael & Patricia Fogden]



Unlike so many of its congeners that show a marked preference for vertical cliffs in which to dig their burrows, Böhm's Bee-eater, a little-studied and very localized African species, always chooses a completely flat area in well-drained sandy ground, by a footpath or a clearing. Chiefly a solitary nester it may also breed in loose colonies of a few pairs, and is not known to have helpers. False starts are uncommon and the straight, gently declining burrow is normally about 1 m long. The clutch consists of 2-4 eggs. One remarkable feature, common to most bee-eaters, is the huge size of the food items so often delivered to feed the chicks, much larger than those currently being eaten by the adults themselves.

[*Merops boehmi*,  
Malawi.

Photo: Brendan Ryan/  
Planet Earth]



in spring has been reported, but it seems to be unusual. A ringed Russian bird was recovered 20 months later in Zimbabwe, nearly 8000 km away, and one ringed in Tunisia in May was found the next day 520 km to the north-west, in Italy.

European Bee-eaters often travel with Blue-cheeked, flocks of the two keeping separate but moving along the same routes at almost the same times. Blue-cheeked Bee-eaters arrive in Zimbabwe in November, when the juveniles are still readily identifiable as such and are even still being fed by adults, as noted by D. Aspinwall and K. Hustler in 1997. In Asia, young Blue-cheeked Bee-eaters leave the nest mainly in late July, so that those arriving in Zimbabwe, originating from central or south-western regions of Asia, seem to have completed the journey, travelling in family parties, in ten weeks or so.

Another great migrant is the Rainbow Bee-eater, which breeds in south Papua New Guinea and in many lightly wooded parts of Australia. This species spends the austral winter, from March to October, in north Australia, south in the eastern coastal lowlands to the northern outskirts of Brisbane, and in the Torres Strait islands, New Guinea, the Lesser Sunda Islands, Sulawesi, and the Moluccan and Bismarck Archipelagos. Migrants travel by day and on moonlit nights, and cross the central spine of mountains in New Guinea by way of passes at 3000-4000 m. The first arrivals back in southern Australia are observed in September and the main body of migrants appears in October, the birds departing northwards again in March. In the austral autumn, in March and April, thousands of Rainbow Bee-eaters fly north over Innisfail on the north-central coast of Queensland, and emigrants concentrate at Torres Strait, in places large flocks following each other without intermission. If headwinds are encountered, there can be huge mortality on islands without fresh water: dehydrated corpses can be found perched in macabre rows on a dead shrub, huddled side by side, falling off or spinning to hang upside-down by their clinging toes if the branch is shaken, or carpeting the ground beneath a clump

of roosting bushes. Some migrants overshoot New Guinea, to appear in Micronesia and the Japanese islands. In May and June, many birds live around Cape York mangroves, departing in July. The main spring passage is in August and September, small flocks travelling south between Darwin and Thursday Island, where up to 860 have been recorded crossing in an hour, flying just above the waves or at heights of up to 100 m.

Finally, it is worth mentioning the widely repeated claim that the Olive Bee-eater migrates between Madagascar and Africa, a fact that has been doubted by many commentators, yet there are grounds for believing that it may be true. Since the Blue-cheeked and Blue-tailed Bee-eaters, with which the Olive forms a superspecies (see Systematics), are highly migratory everywhere, there seems to be reason to suspect that the Olive Bee-eater also migrates between those two parts of its range, but convincing evidence that it does is lacking. It is resident in Madagascar, and may prove to be resident in the Comoro Islands, while in Africa, in various regions, it is resident, partially migratory or a breeding or non-breeding visitor. At extremes in its African range, the Olive Bee-eater is a breeding visitor to south-west Angola and north-west Namibia in September-June, commonest in November-April; a non-breeding visitor to the Mozambique littoral, sometimes breeding south to north Natal, in September-April; a non-breeding migrant in Kenya in May-September and November-March, and an erratically breeding resident there near the coast; and a common resident in north-west Somalia, where it breeds in April and May. Further research and study are required to determine the full extent of movements undertaken by this species.

### *Relationship with Man*

Today, bee-eaters are widely admired by birdwatchers for their diverse and beautiful plumages and for other characters. Many



The Swallow-tailed Bee-eater nests solitarily or in small groups of two or three pairs, digging its burrows in flat or shelving ground with bare, sandy patches. On one occasion three adults were filmed entering one of its nests. How general co-operative breeding is in this species, as indeed in so many others, remains unknown. The value of a helper's aid is unquestionable, though, particularly at times when insects are scarce or prevented from flying by bad weather. Then the extra food that helpers provide may tip the balance in favour of the nestlings' survival.

[*Merops hirundineus*  
*hirundineus*,  
 Kalahari Gemsbok  
 National Park,  
 South Africa.  
 Photo: Richard Du Toit/  
 BBC Natural History Unit]

of the species have pleasant voices and are gregarious and confiding, and they are easy to watch and enjoy because they are conspicuous daytime birds in open countryside. In many well-wooded tropical towns they are also quite common birds of suburban parks and gardens. Rather surprisingly, bee-eaters have not featured very prominently in art, and in European and classical Mediterranean traditions they have been rather overlooked. Only a single representation has been identified in ancient Egyptian art and hieroglyphs, a finely carved relief of a Little Green or perhaps a Blue-cheeked Bee-eater on a wall of Queen Hatshepsut's mortuary temple. A 2000-year-old mural depicting evident Blue-cheeked Bee-eaters was recently unearthed in the fabled Roman villa of Agrippina. An early and beautiful painting of a European Bee-eater is in the Lombard Giovaninno de Grassi's Sketchbook of the late fourteenth century, but in recent centuries bee-eaters have not appealed to artists so much as has, for instance, the Eurasian Kingfisher (*Alcedo atthis*). Various bee-eaters feature on the postage stamps of at least 38 countries worldwide, the European Bee-eater topping the list, with 18 countries, followed by the Carmine Bee-eater, with eleven; for comparison, Eurasian Kingfishers are depicted on stamps in 25 countries and Hoopoes (*Upupa epops*) in no fewer than 43!

A far more important point of contact has been in relation to bee-keeping. The birds are strongly attracted to commercial honeybee hives, and various species have been persecuted by apiculturists because of the inroads that they can make into honeybee stocks.

The natural distribution of honeybees is throughout the warmer parts of the Old World, and Spanish cave paintings 10,000 years old depict scenes of honey-hunting. There are similar cave paintings in Africa, India and Australia. Honey was much esteemed in ancient Egypt; and Aristotle and Virgil wrote about the destructiveness of bee-eaters to hive bees. For millennia, another important product has been beeswax, mainly for candles. In 1910, Russia and Ukraine had 6.75 million honeybee hives, which produced 32,000 tonnes of honey and 4000 tonnes of beeswax.

It is scarcely surprising that European Bee-eaters, which habitually forage around apiaries, have earned themselves much enmity, nor that persecution of them within and outwith the law has been widespread. Large numbers are killed every year in Malta and Egypt, or at least they were until very recently. Fifty years ago, it was fashionable to determine the pest status of an insectivorous bird species by evaluating the "harmful" and the "beneficial" insects which it ate. As a consequence, thousands

of bee-eaters were routinely shot in parts of Europe and Asia. Blue-cheeked Bee-eaters were persecuted by bee-keepers in Iraq at least until the 1970's, but they are less of a nuisance in Russia and Kazakhstan, where they have even been considered economically valuable. In Pakistan and India, agriculturalists formerly regarded the Little Green Bee-eater as beneficial, but after the introduction of apiculture in one region the bird became commoner; 850 were shot, found to have eaten bees, and attitudes hardened. All sorts of control measures have been taken, including the stopping-up of nest-burrows, and poisoning with strychnine, cyanides, carbon disulphide or chloropicrin, but the most widely employed method has been shooting. Hooks baited with live bees dangling from nylon lines threaded around an apiary caught 80 bee-eaters in ten days.

Another approach is evasion rather than destruction. This involves simply shutting bees into the hive, or moving an entire apiary out of harm's way. As many apiculturists recognize, bee-eaters are in some ways beneficial. Bee genera such as *Psithyrus*, *Sphecodes* and *Allodape* are in part themselves predators of honeybees, and bee-eaters prey upon them. Sphecids wasps (*Cerceris*), bee-pirates or bee-wolves (*Philanthus*) and hornets (*Vespa crabro* and *V. orientalis*) can seriously damage honeybee stocks, but all bee-eaters eat those wasps in quantity. An analysis of 47,000 prey items from many countries has shown that the ratio of honeybee-predators to honeybees in the diet of bee-eaters is overall of the order of 6:100. Even when preying on honeybees, bee-eaters may be less harmful than at first appears, since in autumn they tend to kill old bees, which suffer a higher winter mortality from diseases than do young ones. In the wider context, bee-eaters are also valuable for their predation upon locusts and on insect pests of cotton fields and stored products.

### Status and Conservation

Nearly all bee-eaters seem to be holding their own, and no species or subspecies gives cause for serious conservation concern. In the absence of hard and fast information, we can only speculate about past trends. It is, however, likely that the ranges of tropical forest bee-eater species have contracted but that those of all open-country ones, the large majority of taxa, have expanded with the opening-up of native woodland for agriculture. Certainly, nearly all populations remain common in many or most

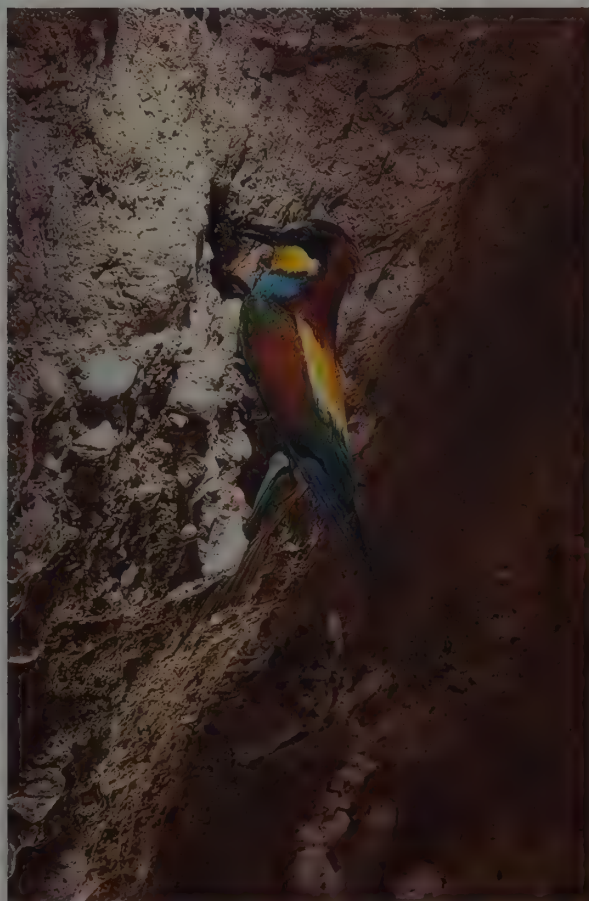




On occasion the European Bee-eater is a solitary breeder though more frequently it forms loose groups of a few pairs or well-defined larger colonies, sometimes sharing a site with other species. In this species, clutch size varies considerably, within the range of 4–10 eggs. If the first clutch fails, a second may be laid, and a fresh hole may even be dug expressly for it! The adult arriving with food calls persistently at the hole entrance and continues to do so as it enters, though the chicks commonly wait near the entrance to be fed, the first one moving back when satisfied, thus making room for the next.

If the first chick fails to move back, its tail is tugged by the next in line until it gives way! Nestlings reach adult weight in 15–17 days, and when they finally leave the nest after about a month they are slightly above adult weight. The adults continue to feed them for a further three weeks, but any youngsters begging after that remain unanswered.

[*Merops apiaster*,  
Alicante, Spain.  
Photos: José B. Ruiz]





parts of their breeding ranges. If the Blue-headed, Black and Red-bearded Bee-eaters are difficult to find, it is not because they are truly rare but just that, like other rainforest birds, they hide themselves well. Böhm's and Black-headed Bee-eaters have somewhat circumscribed ranges, but each is well distributed and locally frequent or common therein. Of well-defined subspecies, that with the smallest range is the race *andamanensis* of the Bay-headed Bee-eater; it is restricted to the Andaman Archipelago, where it was still judged to be common in the mid-1980's.

Forest and open-country bee-eaters alike are particularly prone to human harassment. Even in the remotest regions, it is not uncommon to find a group of nest-burrows some of which have stones blocking the entrance, and others with hoe or hatchet marks. In rural areas, nestlings are sometimes taken for food and adults shot or lured. As T. M. Brooks and J. N. Kirathe have suggested in relation to Blue-headed Bee-eaters in Kakamega Forest, Kenya, such persecution is less likely to threaten a population in the long term than is, for instance, continual trampling by cattle grazing the more open areas in the forest where bee-eaters tend to nest. In India and South-east Asia, too, increasing utilization of native forest for timber, cattle grazing, slash-and-burn agriculture, and even recreation, is likely to have detrimental effects on the densities of forest bee-eaters, while the wholesale replacement of natural forest, by oil palm plantations in Malaysia for example, has catastrophic consequences.

The status of the Carmine Bee-eater in Zimbabwe has been reviewed in the 1990's by P. J. Mundy and colleagues and by P. J. Feather. Counts of nest-holes, not all occupied, suggest that there are 21,000-25,000 birds before breeding, and estimates at roost-sites give some 37,500 birds after breeding. The population is threatened on several fronts. It is vulnerable to disturbance from increasing human settlement and the intensification of land use. Greater use of insecticides may also be detrimental. Human interference and persecution seem to have caused the desertion of several traditional nesting sites. Combined with the silting of major rivers as a result of poor land management, pan-

ning for gold and woodland clearance, the construction of dams and weirs and changes in river-management policies are evidently affecting the physical properties of riverbanks. Soil moisture and structure, and the way in which cliffs are cut every year by water flow, determine the quality of vertical banks for nesting birds. A lowered water table, a shorter flowing season, the drying-out of banks, flash flooding and wash from speedboats all have an adverse effect on a colony's breeding success. It seems that Carmine Bee-eater colonies are becoming concentrated into the national parks and the Zambezi Valley.

In the last few decades, the fortunes of European Bee-eaters have varied and regional breeding densities have waxed and waned. In the 1980's, BirdLife International estimated the European population of this species to be between 86,000 and 380,000 pairs, with numbers decreasing in Portugal, the Czech Republic, Bulgaria and Greece and increasing in Spain, France, Switzerland, Slovakia, Poland, Belarus and Ukraine, and declining somewhat overall. The four largest populations are thought to be those of Portugal, Spain, Bulgaria and Romania, but the estimation limits are narrow only in Spain, where there are considered to be between 23,000 and 30,000 breeding pairs. Portugal's population is probably lower. These values are of the same order of magnitude as estimates in the 1970's of 34,000-37,000 autumn migrants at Gibraltar each year, although J. L. Lopez Gordo reckoned that a million bee-eaters might emigrate from Spain, a little farther west. Sardinia has 3000-5000 breeding pairs, or 12-21 pairs per average 100 km<sup>2</sup> throughout the island. In the early 1990's, there were about 51 breeding pairs per 100 km<sup>2</sup> in Slovakia and 73 per 100 km<sup>2</sup> in Bulgaria, both in prime habitat. In the European breeding-bird atlas, published in 1997, A. Krištin and T. Petrov estimated the total European population to be between 96,000 and 243,000 pairs, with a further 10,000-100,000 in Turkey. On that basis, the global population of the European Bee-eater, including those breeding in Asia and southern Africa, might be between 170,000 and 550,000 pairs.



In bee-eaters the size of the clutch varies not only with species, but also with latitude, ranging from two eggs near the equator to six to ten in temperate regions. The eggs are all similar, pure white and glossy, and are laid at intervals of 1-2 days. Incubation, beginning with the first or second egg lasts 20-26 days. The recently hatched chick emerges pink, blind and naked, but by its second week it is covered in pointed grey spines, rather like a hedgehog, as visible in these Little Green Bee-eaters. With their eyes now open they are alert and obviously mobile, having crawled along the tunnel from the nesting chamber to meet their parent.

[*Merops orientalis orientalis*, Sri Lanka.  
Photo: T. S. Zylva/FLPA]



Most tropical bee-eater species are more or less sedentary, but a few migrate. Outstanding in the latter group is the Carmine Bee-eater. This species performs a rather complex three-stage migration, which is still imperfectly known, especially in the case of the northern, nominate race. The southern race, which never comes into contact with its northern counterpart, breeds in an area from south Angola across to central Mozambique, mainly in September and October; subsequently, it disperses south towards north-eastern South Africa; and, finally, it moves north in advance of the austral winter, May to August, before starting the whole process over again.

[*Merops nubicus nubicus*, Central African Republic. Photo: Mathieu Laboureur/Bios]



Direct destruction may affect European Bee-eater populations locally, but probably does not have an appreciable effect on the species globally. In Cyprus, 4000-6000 of these birds, mainly autumn migrants from the north, are shot every year. Up to one hundred pairs nested there up to the 1970's, but these had been shot out by the early 1980's; a few returned in 1991-1992, when spring shooting was banned. Thousands more are still hunted around the

east Mediterranean, or killed by bird-limers mainly for eating, though some are destined for taxidermy. Overenthusiastic use of insecticides can affect the species adversely, as is known to have happened recently in Senegal, but for this and other bee-eaters it is physical environmental modification that can have the most long-lasting impact. Bee-eaters often nest in riverbanks and hunt over river valleys, and Kristin and Petrov point out that European Bee-eaters decrease where rivers are dredged and canalized with stone revetments and erosion defences. Quarrying of sand and aggregates can destroy breeding sites, although it can also create them, and municipalities and developers should be encouraged to create small fenced-off sand cliffs wherever bee-eaters are liable to be attracted to nest.

At present, no bee-eater species is considered threatened. However, those that are confined to tropical rainforest zones have generally seen their ranges shrink in recent years, owing to habitat destruction. The Purple-bearded Bee-eater, which occurs only on the Indonesian island of Sulawesi, can still be found there in several forest reserves and parks, though it is nowhere common.

[*Meropogon forsteni*, Lore Lindu National Park, Sulawesi. Photo: Bernard van Eiegem]



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1

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PLATE 25

inches 3  
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## Genus *NYCTYORNIS* Jardine & Selby, 1830

### 1. Red-bearded Bee-eater

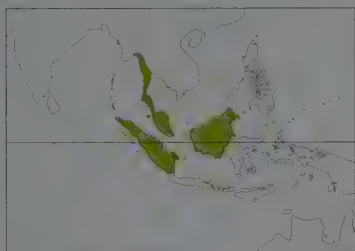
#### *Nyctyornis amictus*

**French:** Guépier à fraise **German:** Rotbartspint **Spanish:** Abejaruco Barbirrojo  
**Other common names:** Red-breasted Bee-eater

**Taxonomy.** *Merops amictus* Temminck, 1824, Bengkulu, Sumatra.

Species name often listed as *amicta*, but genus was originally established without a specified combination, and must therefore, in accordance with International Code of Zoological Nomenclature, be treated as masculine. Monotypic.

**Distribution.** S Myanmar (S from Dawna Range) and SW Thailand (Petchaburi District) S through Malay Peninsula to Johore, including Penang I; also Sumatra and Bangka I, and throughout lowland Borneo.



**Descriptive notes.** 27-31 cm; male 68-92 g, female 61-70 g. Male green above and paler green below; crown lilac of an extraordinary hue, intense and with pearly sheen; bases of lilac feathers buff or red, and from underside tips of feathers appear red, not lilac; narrow border of small, thin, stiff, forward-curving, pale azure feathers around base of bill; throat feathers long and broad, bases grey and dark olive-green, only tips, with long radiating barbs, are red; rectrices rather stiff, with shafts wide proximally and ivory or pale yellow; upperside of tail green, underside yellow with black tip; bill robust,

arched, strongly decurved, blackish, with proximal quarter of lower mandible lead-grey; mouth yellowish; iris bright orange. Female like male, but lilac crown patch smaller; forehead and hindcrown vermilion and green respectively, not lilac. Immature uniform green but for warm buff undersides of wings, yellowish underside of tail, and a few pale blue feathers around base of bill.

**Habitat.** Middle storey and lower part of canopy of lowland evergreen mixed dipterocarp forest, at up to 1500 m; also disturbed forest, forested banks of streams, lagoons and swamps, and in Myanmar well-lit woods; sometimes in gardens and about houses.

**Food and Feeding.** Airborne insects: wasps, hornets, bees including carpenter-bees (*Xylocopa*), cicadas, beetles, crickets and ants. Hunts from elevated leafy perch overlooking open airspace, by flying out after passing insect; sits almost motionless for long period, then moves to new vantage point.

**Breeding.** Eggs in Aug, Jan and Feb and young in Mar-Jun; most clutches have been found in Feb. Excavates nest-hole in earth in roadside bank, in sandy or stiff soil by small stream in dense forest or in cutting or sawyer's pit; burrow c. 1-2 m long. Clutch up to 5 eggs, generally 3; both sexes thought to incubate.

**Movements.** Resident and sedentary.

**Status and Conservation.** Not globally threatened. Density of 4 birds/20 ha of primary lowland forest in Borneo and c. 2/20 ha in peninsular Malaysian forest. Absent from large swathes of its former range where dipterocarp forest has been replaced by oil palm and rubber plantations, as in Malaysian states of Perak, Selangor, Negri Sembilan, Malacca and Johore. Present in many national parks, e.g. Kaeng Krachan (Thailand), Taman Negara (Peninsular Malaysia), Kerinci-Seblat and Way Kambas (Sumatra) and Gunung Mulu (Sarawak).

**Bibliography.** Auber (1959), Baker (1934b), Chasen & Hoogerwerf (1941), Fogden (1976), Glenister (1971), Gore (1968), Holmes (1996), Hume & Davison (1978), Inskipp *et al.* (1996), Jeyarajasingam & Pearson (1999), Lekagul & Round (1991), MacKinnon & Phillips (1993), Madoc (1976), van Marle & Voous (1988), Medway & Wells (1976), Pearson (1975c), Riley (1938), Robson (2000a), Round (1988), Smythies (1986, 1999), Thompson (1966), Wells (1990, 1999).

### 2. Blue-bearded Bee-eater

#### *Nyctyornis athertoni*

**French:** Guépier à barbe bleue **German:** Blaubartspint **Spanish:** Abejaruco Barbiazul

**Taxonomy.** *Merops athertoni* Jardine and Selby, 1830, India.

Two subspecies recognized.

**Subspecies and Distribution.**

*N. a. athertoni* (Jardine & Selby, 1830) - W, E & N India (Western & Eastern Ghats, S Himalayas) E to Indochina.

*N. a. brevicaudatus* (Koelz, 1939) - Hainan.



**Descriptive notes.** 31-35 cm; male 85-93 g, female 70-91 g. Forehead pale azure-blue; throat feathers long and broad, forming pendent beard, the feathers dark blue, grading to pure azure-blue on long radiating barbs at tip; upperparts otherwise mainly green when fresh, fading or bleaching to bluish on crown, nape, mantle and tertials; wing-linings warm buff, belly rich buff with broad green streaking; mouth greyish-pink; lores and ring of featherlets around eye green; iris bright orange. Indian birds tend to have clearer green upperparts, paler cheeks and less heavily striped underparts than Indochinese ones, the

difference seemingly clinal. Sexes alike. Immature said to be exactly like adult, but iris probably brown. Race *brevicaudatus* somewhat shorter-tailed and with throat richer blue, but otherwise very similar to nominate race.

**Habitat.** Occupies middle storey of moist deciduous and thick secondary evergreen forest in foothills dissected by ravines; also frequently found in moss-forest, forest clearings with scattered trees and gardens, and thin deciduous hilltop jungle with clearings. Recorded from sea-level up to 2200 m.

**Food and Feeding.** Feeds mainly on flying insects, mainly honeybees, carpenter-bees (*Xylocopa*), wasps including some measuring up to 4 cm, large beetles, dragonflies; woodlice found in one stomach. Paired birds spend much time perched stolidly at or near outer side of tree, sometimes on top of tall tree, but hawking sorties have seldom been seen; some evidence that it searches tree holes and blossoms for insects.

**Breeding.** Clutches found in Assam in Feb-May and Aug, in Nepal in Apr-May and Oct, in Myanmar in Apr but breeding takes place from Mar to Oct, and in Thailand about Apr-May. Excavates burrow in bank by forest path, sandy bank of stream, road cutting, or precipitous alluvial cliff face of forest ravine or earthslip; burrow 1.3-3.0 m long, round in cross-section, 75-95 mm in diameter, straight, level or slightly inclining, ending in unlined egg-chamber 20 cm wide and 13 cm high. Clutch up to 6 eggs; feathered nestling not described; no further details available.

**Movements.** Resident; in general appears to be sedentary, but seasonal fluctuations in numbers reported in Nepal, Eastern Ghats of India, Myanmar and SE Thailand, perhaps the result of local movements or of vertical migration.

**Status and Conservation.** Not globally threatened. Fairly common in lower Himalayas, W to Kotgarh; sparingly distributed in Myanmar, S along coast to Kyaikkami; uncommon or local in Thailand; very local in Western Ghats of India, from Gujarat Satpuras and R Tapti to W Maharashtra, Karnataka, Patni Hills in Tamil Nadu, and Kerala. In Eastern Ghats, recorded near Lamasingshi on only 24 out of 221 days of field observation. Present in numerous national parks, e.g. Corbett, Kaziranga, Namdapha and Mudumalai (India), Chitwan (Nepal), Doi Inthanon, Nam Nao and Khao Yai (Thailand) and Nam Bai Cat Tien (Vietnam).

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## Genus *MEROPOGON* Bonaparte, 1850

### 3. Purple-bearded Bee-eater

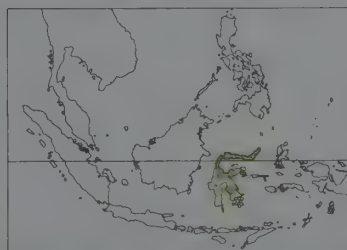
#### *Meropogon forsteni*

**French:** Guépier des Célèbes **German:** Celebesspint **Spanish:** Abejaruco de Célebes  
**Other common names:** Sulawesi/Celebes (Bearded) Bee-eater

**Taxonomy.** *Meropogon forsteni* Bonaparte, 1850, Sulawesi.

Bears startling resemblance to W African *Merops breweri* in some aspects of plumage and long, attenuated central rectrices, but bill shape and beardness differ, and there is no good reason to suppose that the two are closely related. Monotypic.

**Distribution.** Locally in N, C & SE Sulawesi.



**Descriptive notes.** 25-26 cm (with streamers, up to 6 cm more). Forehead and crown blackish, feathers with ultramarine fringes; lores blue-black; ear-coverts, nape and sides of neck chocolate-brown or dark vinous-brown; purple throat feathers broad, long and overlapping breast, not drooping, though bird looks full-chested; chin and neck feathers commonly erected to form ruff or cape at front and sides of neck; upperparts and wings green, wings short; lower belly dark brown to somewhat variable extent; tail with central rectrices green and ending in narrow streamers, outer vane of outer rectrix entirely green, other tail

feathers russet, narrowly edged and tipped green; underside of tail dull russet, shafts ochreous; bill slender, not strongly decurved, shape like bill of *Merops persicus*, black; iris dark brown. Female very similar to male, but tail-streamers perhaps somewhat shorter; dark brown generally extends further up belly. Immature similar to adult, but head and breast mostly green, only feathers of lower throat and upper breast dark blue, not much elongated, and central rectrices do not form streamers.

**Habitat.** Openings and clearings in primary and successional forest, from sea-level to 1850 m; edges of lowland, montane and elfin moss-forest; occasionally farmland with plenty of large trees.

**Food and Feeding.** Diet consists of airborne insects, including honeybees, other bees, wasps, beetles and large dragonflies. Uses treetop perch as lookout for food, when bird is alert and lively, twisting and turning head, searching in all directions; prey caught in short sallies; bird returns to perch with prey, mandibulates it with bill inclined upwards, then beats it a few times against perch.

**Breeding.** Mar, Sept and Nov; occupied nests recorded in Jul and Sept. Excavates burrow in steep bank by forest stream, cliff, landslip, road cutting, or bank by forest path; one burrow was 40 cm long, another 90 cm long with entrance 90 mm wide and 35 mm high. No further information available.

**Movements.** Resident or partial migrant, said to move near to coast for the rains, returning inland to breed in dry season.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in Sulawesi EBA. Nowhere very common, but not particularly rare in Tangkoko and Ambang Mountain Reserves; present in Dumoga-Bone and Lore Lindu National Parks and Morowali Reserve, and in several other forests in C Sulawesi; early records from Tondano, Masarang, Mahawu Massif, Mengkoka Range, Mongondo, Takala Mts, Rurukan, Wawo, Masembo and Tanke Salokko.



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## Genus *MEROPS* Linnaeus, 1758

### 4. Black-headed Bee-eater

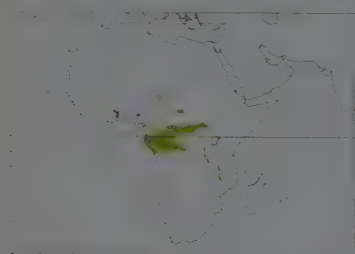
#### *Merops breweri*

**French:** Guépier à tête noire **German:** Schwarzkopfspint **Spanish:** Abejaruco Cabecinegro

**Taxonomy.** *Meropogon Breweri* Cassin, 1859, Ogobai River, Gabon.

Has been placed in monotypic genus *Bombylonax* on account of its robust bill and some similarities to *Meropogon forsteni*; its biology, however, is now better known, and it appears to be a typical *Merops*. Monotypic.

**Distribution.** SE Nigeria (Igalaland Plateau); N Central African Republic (near Ndélé); Gabon, Cabinda (N Angola), Congo and E Zaire (Kinshasa to Bandundu on R Kasai, N to Bangui and E to Bamili on R Uele, E to Banalia on R Aruwimi); and NE Zaire (near Etiga) and SW Sudan (Bangangai Forest). Formerly also SC Ghana; recently recorded in Ivory Coast.



**Descriptive notes.** 28 cm (with streamers, up to 6 cm more); 54 g. Head black; back and wings green; tail with long central feathers, upperside green and cinnamon, underside dull dark cinnamon; underparts rich ochre with cinnamon breastband, latter narrower in centre than at sides, where it can be concealed by wings; bill black, more robust than in any congener except the large *M. nubicus*; iris brilliant crimson; legs and feet dark grey, soles of feet yellow, claws black. Very similar to *Meropogon forsteni* in colour, pattern and shape of tail, but differs in cinnamon-ochre underparts, absence of purple tones. Sexes

alike. Immature like adult, but central tail feathers not elongated, has black feathers of forehead, crown and nape broadly fringed green, sometimes a distinct green moustachial streak, lacks cinnamon band across breast, which is green-washed; fledgling has broad green outer edges to all rectrices.

**Habitat.** Forest edge, open secondary growth, plantations, around clearings and dwellings in forest, particularly near rivers and streams; wooded islands and riverbanks; gallery forest and swamp-forest, nesting adjacent in dry savanna.

**Food and Feeding.** Diet consists of airborne insects, mainly bees and wasps; also chafers, dung beetles and other beetles; a few very large wasps and dragonflies; and cicadas, hawkmoths, butterflies; grubs probably given to nestlings. Prey caught in short sallies at low and mid-levels, up to 5 m above ground, in dense or open woodland; snatches a few insects from ground layer of vegetation.

**Breeding.** In N portion of range excavates burrows in Jan, lays in Feb; in S, lays in late Aug and, especially, Sept. Nests solitary or in loose colonies, e.g. 13 were located nests along 2 km of forest/savanna boundary, several only 12–100 m apart. Breeds in pairs or trios of adults. Excavates burrow in sloping heap of soft lateritic earth, in termite mound, or in bare or grassy sandy ground in cultivated field or fire-blackened grassland; burrow declines at c. 20° to horizontal, round or oval in cross-section, c. 55 mm high and 65 mm wide, with entrance 70–90 mm in diameter, more or less straight and 1.1–2.1 m long, and ending in egg-chamber sharply angled to one side, oval, 25 cm long. Clutch 2 or 3 eggs; female alone thought to incubate; nestlings fed by both or all adults.

**Movements.** Resident or locally migratory. Not usually gregarious, but a flock of 40 in W Congo may have been migrating.

**Status and Conservation.** Not globally threatened. In most areas regarded as a rarity, but has probably been widely overlooked. Common breeder at Ménengué, in Kouilou Basin, SW Congo. Nests there in fire-blackened ground had piles of excavated yellow sand at entrance, making them very conspicuous; nesting failure extensive, people snaring adults or wilfully blocking up nest entrances; planting of Ménengué area with eucalyptus, projected in 1991, could bring about local extinction. Formerly also occurred in Ghana, in riverine forest along R Afram, but species disappeared when this zone was inundated as part of I. Volta in 1966. First record from Ivory Coast in 1998, during survey of Marahoué National Park.

**Bibliography** Bannerman (1953), Bouet (1961), Dean (2000), Demy (2000a), Dowsett & Dowsett-Lemaire (1991, 1993, 1997), Dowsett & Forbes-Watson (1993), Dyer *et al.* (1982), Elgood *et al.* (1994), Fry & Gilbert (1983), Fry *et al.* (1988), Green (1984), Green & Carroll (1991), Grimes (1987), Hendrick (1980), Hockey (1996), Horwood (1964), Lippens & Wille (1976), Mackworth-Praed & Grant (1970), Maes & Louette (1983), Malbrant (1952), Nikolaus (1987), Pinto (1983), Schouteden (1962), Serle (1957), Snow (1978, 1979), Traylor & Archer (1982).

### 5. Blue-headed Bee-eater

#### *Merops muelleri*

**French:** Guépier à tête bleue **German:** Saphirspint **Spanish:** Abejaruco Cabeciazul

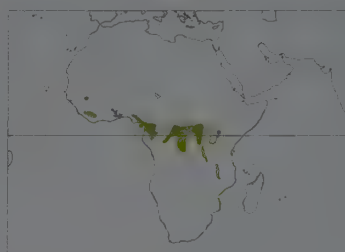
**Taxonomy.** *Meropiscus Müllerii* Cassin, 1857, Muni River, Gabon.

Formerly sometimes joined with *M. gularis* in genus *Meropiscus*. Has been placed with other small, round-winged species lacking tail-streamers in genus *Mellitophagus*, comprising present species and *M. gularis*, *M. pusillus*, *M. variegatus*, *M. oreobates*, *M. bulcocki* and *M. bulcockoides*. Races intergrade between R Cross, Nigeria, and Douala, Cameroon; Kenyan population has been described as race *valensis*, but now considered indistinguishable from nominate. Two subspecies currently recognized.

**Subspecies and Distribution.**

*M. m. mentalis* Cabanis, 1889 - Sierra Leone and SW Mali to W Cameroon, and Bioko (Fernando Póo). *M. m. muelleri* (Cassin, 1857) - S Cameroon and N Gabon to E Zaire, also W Kenya.

**Descriptive notes.** 19 cm (*mentalis*, with streamers, up to 3 cm more); 18–25 g. Male of nominate race has pointed white forehead feathers, pale blue crown, purple-blue nape, black sides of head;



red chin feathers stiff and narrow, the barbs not radiating but forming a straight tuft; upperparts and wings deep chestnut; tail square-ended, appears blue above when closed but concealed parts are black; tail black below; underparts purplish-blue; iris dark red-brown. Female generally very similar to male, but some individuals have olive wash on chestnut parts and green wash on blue parts; red chin patch smaller; iris wine-red. Immature has chestnut parts more ochreous than adult and blue parts more a dusky turquoise, with crown, cheeks and mantle washed olive. Race *mentalis* differs in darker purple-blue to

turquoise forehead, crown and cheeks, paler blue underparts, and elongated central rectrices with club-shaped tips.

**Habitat.** Lowland rainforest, often within forest interior, but also around clearings and glades, along paths or at forest edge; also hunts in tilled land with only a few dead trees left standing. Occurs at up to 1200 m on Bioko.

**Food and Feeding.** Prey includes honeybees, ichneumons, ants, other hymenopterans, butterflies, moths, orthopterans, beetles and tabanid flies, all taken on wing; butterflies common prey in Sierra Leone. Makes short, fly-catching sorties from low down or high up, mainly within 4 m of ground in thick woody growth, sweeping low after passing insect, seizing it and wheeling back to same perch; 55% of sallies result in successful catch. Bees typically beaten and rubbed against perch.

**Breeding.** Fledglings seen in Feb in Sierra Leone, eggs in Jan in Cameroon; probably breeds about Jan–May in Kenya. Excavates burrow in roadside bank, in side of sawyer's pit on forest floor, or in soil raised around roots of large tree.

**Movements.** Resident.

**Status and Conservation.** Not globally threatened. In Sierra Leone not uncommon in Gola Forest; in Liberia only found on Mt Nimba, where uncommon; uncommon in Ivory Coast; rare in Nigeria; quite common on Bioko; sparse to locally common in Zaire. Range of outlying population in Kenya has contracted; formerly recorded at Nyarondo, Lerundo and Elgon, now probably restricted to Kakamega and South Nandi Forests, where uncommon. Kakamega birds persecuted by stone-throwing boys, but considerably more serious threat posed by significant inroads resulting from farming, and also trampling by cattle, which now graze throughout the forest. Species present in a number of national parks, e.g. Tai Forest (Ivory Coast), Cross River (Nigeria), Korup (Cameroon) and La Lopé (Gabon).

**Bibliography** Amadon (1953), Ash (1990), Bannerman (1933, 1953), Bennun & Njoroge (1999), Britton (1980), Brooks & Kiratthe (1997), Carter & Dickerman (1988), Chapin (1939), Cheke & Walsh (1996), Christy & Clarke (1994), Colston & Curry-Lindahl (1986), Demy & Fishpool (1994), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgood *et al.* (1994), Field (1999), Fry *et al.* (1988), Gatter (1997), Grimes (1987), Hockey (1996), Imboma *et al.* (1996), Lewis & Pomeroy (1989), Lippens & Wille (1976), Mackworth-Praed & Grant (1957, 1970), Njoroge (1994), Pérez del Val (1996), Robertson (1995b), Short *et al.* (1990), Snow (1978), Zimmerman (1972), Zimmerman *et al.* (1996).

### 6. Black Bee-eater

#### *Merops gularis*

**French:** Guépier noir **German:** Purpurspint **Spanish:** Abejaruco Negro

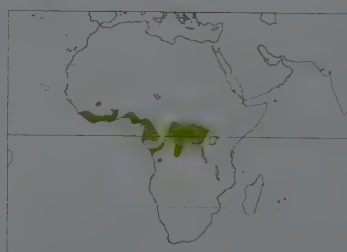
**Taxonomy.** *Merops gularis* Shaw, 1798, Sierra Leone.

Formerly sometimes joined with *M. muelleri* in genus *Meropiscus*. Has been placed with other small, round-winged species lacking tail-streamers in genus *Mellitophagus*, comprising present species and *M. muelleri*, *M. pusillus*, *M. variegatus*, *M. oreobates*, *M. bulcocki* and *M. bulcockoides*. Races intergrade in SE Nigeria. Two subspecies recognized.

**Subspecies and Distribution.**

*M. g. gularis* Shaw, 1798 - Sierra Leone, SE Guinea and S Mali E to SE Nigeria.

*M. g. australis* (Reichenow, 1885) - SE Nigeria or W Cameroon through Congo Basin to W Uganda and N Angola.



**Descriptive notes.** 20 cm; 25–34 g. Nominata race has black head with blue forehead and supercilium, and often a blue line below eye; scarlet throat feathers with basal part dark grey and diamond-shaped, tips consisting of 10-mm-long tuft of non-interlocking barbs; upperparts black, except for brilliant azure-blue rump and uppertail-coverts (as vivid as in many alcedinids); uppertail-coverts long; remiges dark rufous with blackish tips; wing-coverts and secondaries narrowly edged green to azure-blue and tertials broadly tipped green to azure-blue, wearing or bleaching to blue; breast black with blue streaks, belly and undertail-coverts, latter

very long, brilliant blue (as rump). Sexes alike. Juvenile similar to adult, but chin and throat oily dark green, breast dull black, belly and undertail-coverts less brightly azure. Race *australis* lacks blue forehead, supercilia and blue below eye, sometimes showing red feather tips on breast.

**Habitat.** Edges of high forest next to cleared land, plantations, waterways and larger clearings in rainforest; secondary and fringing forest, mesic savanna woodland with well-formed canopy, oil palm bush, and edges of gallery forest in savanna. Uses dead trees and telephone wires as sentinel feeding posts.

**Food and Feeding.** Diet consists of airborne insects: hymenopterans including honeybees, other bees, wasps, and ants, also butterflies, dragonflies, damselflies, dipteran flies, moths, bugs, beetles and a few grasshoppers and crickets. Forages by keeping watch from elevated perch and dashing out after passing insect, thereafter gliding back to perch, where immobilizes prey by beating it.

**Breeding.** Feb–Mar in Sierra Leone; in Ghana, Nigeria and Cameroon burrow excavated in or after Jan and eggs laid in Mar–May; in Zaire (Ituri) breeds in Jan–Apr, and farther S inferred to breed in Jan–Sept. Nests solitary in most of range, but in small colonies in Sierra Leone and Liberia; in Liberia (Mt Nimba) 6–12 birds inhabited same site for 2–3 years, and 12 adults occupied at least 2 nest-holes in Mar 1979 whereas there were 8 holes in Mar 1981. Nest-burrow dug at the side of a shallow ditch, in the shallow bank of a small forest stream, in low embankment in oil palm or



rubber plantation, or in old termite hill; burrow 38-65 cm long; one burrow sloped upwards, then downwards at end into egg-chamber. Clutch of 2 eggs. No further information available.

**Movements.** Resident and partial migrant. Best evidence for migration comes from Mt Nimba, Liberia, where there is a regular influx of birds coinciding with the onset of the rains in Feb-Mar, when flock after flock of 10-30 individuals can be seen flying W during the early parts of those months, whereas numbers decrease during dry season, Nov-Dec. Species vacates Bo, in SE Sierra Leone, from mid-May to mid-Aug. Also absent from some parts of Ivory Coast during wet season, approximately May-Jun. Further investigation required.

**Status and Conservation.** Not globally threatened. Common in E Sierra Leone, and frequent and widespread throughout most of range; fairly common in R Congo forests; common or numerous in

Bwamba Forest, Uganda. Present in some national parks, e.g. Tai Forest (Ivory Coast), Mount Kupé (Cameroon), La Lopé (Gabon) and Bwindi Forest (Uganda); also in Gola Forests Reserves (Sierra Leone).

**Bibliography.** Bannerman (1933, 1953), Bates (1909, 1927), Britton (1980), Chapin (1939), Cheke & Walsh (1996), Christy & Clarke (1994), Colston & Curry-Lindahl (1986), Dean (2000), Demey & Fishpool (1994), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgood *et al.* (1994), Field (1999), Friedmann & Williams (1971), Fry *et al.* (1988), Gartshore (1984), Gass (1963), Gatter (1997), Grimes (1987), Hockey (1996), Keith (1968), Lippens & Wille (1976), Mackworth-Praed & Grant (1957, 1962, 1970), Mann (1976), Marchant (1942), Pinto (1983), Prigogine (1972), de Ruiter (1993b), Serle (1954, 1958), Short *et al.* (1990), Snow (1978), Thiollay (1971a, 1976), Traylor (1963), Walsh *et al.* (1990).



ssp  
cyanostictus

ssp pusillus

8

ssp  
ocularis

ssp  
meridionalis

ssp  
hirundineus

ssp  
chrysolaimus

7

ssp  
heuglini

9

ssp lafresnayii

ssp variegatus

ssp bangweoloensis

13

10

ssp  
bulocki

12

with  
yellow  
throat

11

ssp  
frenatus

ssp viridissimus

♂

ssp orientalis

♂

♀

16

14

15

ssp cyanophrys

♂

ssp muscatensis

♂

ssp ferrugiceps

♂

PLATE 26

inches 3  
cm 8



## 7. Swallow-tailed Bee-eater

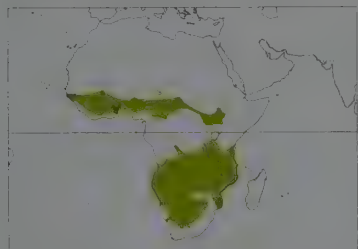
*Merops hirundineus*

French: Guépier à queue d'aronde

Spanish: Abejaruco Golondrina

German: Schwalbenschwanzspint

**Taxonomy.** *Merops hirundineus* A. A. H. Lichtenstein, 1793, Oranje River, South Africa. Has been placed in monotypic genus *Dicrocerus* on account of its tail shape; this appears, however, to be merely an exaggeration of the incipiently fish-tailed shape shown by *M. pusillus*, *M. variegatus* and *M. oreobates*, to which all other morphological and biological characters indicate present species to be closely allied. Four subspecies recognized.

**Subspecies and Distribution.***M. h. chrysolaimus* Jardine & Selby, 1830 - Senegal E to N Central African Republic.*M. h. heuglini* (Neumann, 1906) - NE Zaire, N Uganda, S Sudan and SW Ethiopia.*M. h. furcatus* Stanley, 1814 - S Zaire, N Tanzania and SE Kenya S to C Angola and Mozambique.*M. h. hirundineus* A. A. H. Lichtenstein, 1793 - S Angola, SW Zambia and W Zimbabwe S to S South Africa (Cape Province).

**Descriptive notes.** 23 cm; 18-29 g. Green above, with blue rump; broad black eyestripe edged with bluish-white below; throat yellow, bordered below by blue gorget; breast green, shading to blue on belly and undertail-coverts; remiges mainly rufous, trailing edge of wing blackish; underside of wing pale rufous; exposed parts of tertiaries bleach to greyish-blue; tail deeply forked, middle pair of feathers greyish-blue, remainder greenish-blue, all but median and attenuated outer pair broadly tipped with greyish-white on inner web and with subterminal dusky zone on both webs; outer edge of tail almost straight, the forked

tips curving slightly inwards, fork 31-46 mm deep; iris orange-red to crimson. Sexes alike. Juvenile duller, throat greenish-white, no gorget, iris dark brown. Races differ in breadth of blue gorget and in depth of blue wash on tail and belly: *furcatus* darker than nominate, gorget deeper blue and broader; *chrysolaimus* has pale blue forehead and eyebrow, green on tail; *heuglini* deeper blue on forehead, gorget and tail-coverts.

**Habitat.** Tall, mature savanna woodland; *Baikiaea* woodland on Kalahari sand, *Isobertlinia*, *Calophosphum*, *Brachystegia* and *Combretum* woods, riverine thickets, tall eucalypt windbreaks, bushy river plains, parkland, and semi-desert with scattered *Acacia*. Somewhat nomadic, and readily invades recently burnt areas.

**Food and Feeding.** Diet of honeybees and other hymenopterans, flies, beetles, butterflies, bugs, grasshoppers and cicadas. Feeds by fly-catching in same manner as other small bee-eaters, but perches higher, up to 20 m above ground on bare limb or telephone wire.

**Breeding.** In N tropics breeds about Apr-Jul, and in S Africa in Sept-Dec. Nests solitary, or sometimes 2-3 pairs close together. Excavates burrow in flat or shelving ground with bare patches of sandy soil, or in roadside bank or aardvark (*Orycteropus afer*) lair; burrow 80-100 cm long. Clutch of 2-4 eggs; incubation and nestling periods unknown.

**Movements.** Mobile and nomadic. Movements poorly understood in N tropics, and difficult to interpret even in those parts of S Africa where species is commonest and well watched; seasonal mapping shows it to be commoner in Namibia in Sept-Apr than in May-Aug, but not much seasonal change in Zimbabwe and Zambia, where it has been thought of as mainly a dry-season or Jun-Sept visitor; prone to vagrancy into SE South Africa about May-Aug, with sufficient records in Zululand and Natal for it to be regarded as a winter visitor there.

**Status and Conservation.** Not globally threatened. Widely distributed but local and generally uncommon in N tropics; much larger range S of equator, where sparse and uncommon to locally common; near Lusaka, Zambia, density of 2 birds/km<sup>2</sup> in prime habitat. Present in numerous national parks, e.g. Gombe (Ivory Coast), Bamingui-Bangoran (Central African Republic), Kabalega Falls (Uganda), Mikumi (Tanzania), Liwonde (Malawi), Waterberg Plateau and Etosha (Namibia) and Hwange (Zimbabwe).

**Bibliography.** Anon. (1998b), Bannerman (1953), Barbour (1973), Barlow *et al.* (1997), Beasley (1986), Bennun & Njoroge (1996), Benson & Benson (1977), Benson *et al.* (1971), Boddam-Whetham (1971), Britton (1980), Brown & Britton (1980), Burger (2000), Cave & Macdonald (1955), Cheke & Walsh (1996), Dean (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgood, Fry & Dowsett (1973), Elgood, Heigham *et al.* (1994), Field (1999), Fry *et al.* (1988), Garland (1970), Gass (1963), Ginn *et al.* (1989), Gore (1990), Grimes (1987), Hanmer (1980a), Harrison *et al.* (1997), Harwin & Rockingham-Gill (1981), Hockey (1996), Irwin (1981), Lewis & Pomeroy (1989), Lippens & Wille (1976), Louette (1981b), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Medland (1992b), Morel & Morel (1982), van Niekerk (1992), Nikolaus (1987), Paxton (1987), Penry (1994), Pinto (1983), Pocock (1961), Short *et al.* (1990), Skead (1967), Skinner (1996), Snow (1978), Taylor, P.B. (1979), Thiollay (1971a), Vernon (1968), Winterbottom (1960, 1966), Wolfaardt (1992), Zimmerman *et al.* (1996).

## 8. Little Bee-eater

*Merops pusillus*

French: Guépier nain

German: Zwergspint

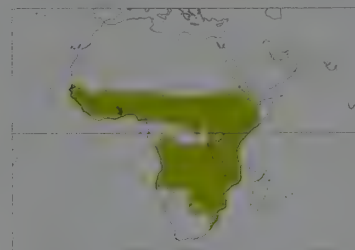
Spanish: Abejaruco Chico

**Taxonomy.** *Merops pusillus* P. L. S. Müller, 1776, Senegal.

Has been placed with other small, round-winged species lacking tail-streamers in genus *Mellitophagus*, comprising present species and *M. muelleri*, *M. gularis*, *M. variegatus*, *M. oreobates*, *M. bulcocki* and *M. bulcockoides*. Races all intergrade along narrow corridor where respective ranges meet. Five subspecies recognized.

**Subspecies and Distribution.***M. p. pusillus* P. L. S. Müller, 1776 - Senegal and Guinea E to C Sudan (to c. 29° E).*M. p. ocularis* (Reichenow, 1900) - from C Sudan E to Red Sea coast of Eritrea, S to NE Zaire and NW Uganda.*M. p. cyanostictus* Cabanis, 1869 - Somalia and E Kenya.

*M. p. meridionalis* (Sharpe, 1892) - E Africa (except E Kenya), and from equator S to Angola and Natal.  
*M. p. argutus* Clancey, 1967 - SW Angola, N Namibia, N & E Botswana, SW Zimbabwe.



**Descriptive notes.** 16-17 cm; 13-19 g. The smallest bee-eater. Crown and upperparts green; broad black eyestripe; cheeks and throat yellow, bordered below by black gorget with cinnamon band below that; rest of underparts rich buff; some rufous in wings, secondaries tipped black; green tertiaries tend to wear or fade to bluish; iris red. Differs from very similar *M. variegatus* in having little or no white bordering yellow cheeks; from *M. oreobates* in much smaller size, less rich colours and little or no white bordering yellow cheeks. Sexes alike. Juvenile lacks black gorget, has pale yellowish-buff chin and throat

merging into light green breast and buff flanks and belly; breast faintly mottled or streaked, upper breast washed with brown. Racial differences rather slight: *cyanostictus* has blue forehead and supercilium, narrow purple-blue line between throat and gorget; *meridionalis* has thin, short blue supercilium, very narrow bluish-white line above gorget; *argutus* and *ocularis* paler than *meridionalis*, former with slightly smaller gorget and latter with somewhat less pronounced supercilium.

**Habitat.** Grassy places, seldom far from water; in dry season frequents marshes, lakeshores, riverbanks, streambanks, and in wet season also cultivated land, lightly and sometimes heavily wooded savanna, grassy clearings in forest, bushy sand dunes, grassy rock outcrops, and treeless plains. Particularly favours drying-out marshes with waist-high grasses and sedges interspersed with woody *Mimosa pigra* thickets. Quick to spread into cleared land in forest, where *Panicum* and other grasses are invading.

**Food and Feeding.** Feeds on large variety of small insects taken on wing, mainly 4-5-12 mm long, some up to 30 mm long; mostly honeybees, *Trigona* bees, halictid bees, ants, digger wasps, spider-hunting and vespid wasps, ichneumonids, and chalcidoid and scolioid wasps; also beetles, flies, damselflies, crickets, pygmy mole-cricket, bugs, butterflies, mayflies, ant-lions (Myrmelionidae), termites and cockroaches. Hymenoptera comprise 40-75% of diet. Forages up to 20 m above ground but mainly low down, perching on grass stems or at side of thorn shrub and hawking just above soil or the herb layer. Watches from perch, often in pairs, for passing insects and gives more or less horizontal chase; most prey taken within a few metres of perch; sometimes "fly-catches" diagonally upwards. Generally makes c. 40 forays/hour, with roughly one-third being successful.

**Breeding.** fledglings seen Feb-Jul in Sierra Leone; eggs in Jan in Mali; in Nigeria laying starts later with increasing latitude, from Mar in C Nigeria to early Jul in extreme N, towards end of cool, dry season; in E Africa lays in all months, around Nairobi mainly in Sept; farther S, Sept-Oct in Zambia, Sept-Feb in Zimbabwe, Sept-Nov (mainly Oct) in South Africa. Excavates solitary nest-burrow, 100 cm long, in low sand cliff, tall cliff, near colony of another *Merops* species, in side of drainage ditch or plough furrow, in gently sloping soil, in flat ground in lee of small tussock or dry herbivore dung, or in side of dried-out hoof mark of large mammal; where aardvarks (*Orycteropus afer*) common, often in sloping roof just inside entrance of lair. Clutch of 4-6 eggs, average 4-4 in Nigeria. Incubation 18-20 days, mainly by female, starting with first egg; first and second eggs hatch within hours on same day, third egg c. 19 hours later, fourth 24 hours after third; nestling period 23-24 days.

**Movements.** Resident, and sedentary or locally dispersive and nomadic. Seasonal shifts in abundance at a given locality often noticed, and new data suggest some partial migration out of Botswana and into Zimbabwe and Transvaal at beginning of austral winter; however, no ringing or other good evidence for long-distance migration.

**Status and Conservation.** Not globally threatened. Throughout its vast range, common in suitable habitat by permanent water but often thinly distributed elsewhere. Density around Zaria, N Nigeria, estimated at 580 birds/100 km<sup>2</sup> in 1970's; extrapolating to all African grassland range would give population of order of 85,000,000. Density in broadleaf woodland at Nyilsivlei, Transvaal, of 1 pair/50 ha. Like many small insectivorous birds, this species is adversely affected by insecticide spraying, both aerial and from knapsack, for tsetse-fly control. Present in numerous national parks, e.g. Saloum Delta (Senegal), Dinder (Sudan), Awash (Ethiopia), Ruwenzori (Uganda), Nairobi (Kenya), Akagera (Rwanda), Mikumi (Tanzania), South Luangwa (Zambia), Liwonde (Malawi) and Kruger (South Africa).

**Bibliography.** Anon. (1998b), Archer & Goldman (1937-1961), Ash & Miskell (1998), Bannerman (1933, 1953), Barlow *et al.* (1997), Benson & Benson (1977), Benson *et al.* (1971), Britton (1968, 1980), Carter (1978), Cave & Macdonald (1955), Cheke & Walsh (1996), Clancey (1967), Colston & Curry-Lindahl (1986), Dean (1971, 2000), Douthwaite (1986), Douthwaite & Fry (1982), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dyer (1979, 1984), Elgood, Fry & Dowsett (1973), Elgood, Heigham *et al.* (1994), Field (1999), Friedmann (1930a), Fry (1972), Fry *et al.* (1988), García (1975), Gass (1963), Gatter (1997), Ginn *et al.* (1989), Giraudoux *et al.* (1988), Gore (1990), Grimes (1987), Hanmer (1980a, 1982), Harrison *et al.* (1997), Hockey (1996), Howland (1987), Irwin (1981), Jones (1979), Lamarche (1980), Lewis & Pomeroy (1989), Lippens & Wille (1976), Lynes (1925), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Marchant (1953), McCulloch (1961), Nikolaus (1987), Penry (1994), Pinto (1983), de Ruiter (1993b), Rutgers & Norms (1977), Serle (1943, 1950b), Short *et al.* (1990), Skinner (1996), Smith (1957), Snow (1978), Steyn (1996b), Tarboton *et al.* (1987), Thiollay (1971a), Tree (1963b), Zimmerman *et al.* (1996).

## 9. Blue-breasted Bee-eater

*Merops variegatus*

French: Guépier à collier bleu

German: Blaubrüstspint

Spanish: Abejaruco Pechiazul

Other common names: Ethiopian Bee-eater (*lafresnayii*)

**Taxonomy.** *Merops variegatus* Vieillot, 1817, Malimbe, Cabinda, Angola.

Has been placed with other small, round-winged species lacking tail-streamers in genus *Mellitophagus*, comprising present species and *M. muelleri*, *M. gularis*, *M. pusillus*, *M. oreobates*, *M. bulcocki* and *M. bulcockoides*. Sometimes regarded as forming a superspecies with *M. oreobates*; although there is some geographical overlap between them, they are segregated altitudinally. Race *lafresnayii* sometimes treated as full species or, alternatively, as belonging in *M. oreobates*, but

On following pages: 10. Cinnamon-chested Bee-eater (*Merops oreobates*); 11. Red-throated Bee-eater (*Merops bulcocki*); 12. White-fronted Bee-eater (*Merops bulcockoides*); 13. Somali Bee-eater (*Merops revoilii*); 14. White-throated Bee-eater (*Merops albicollis*); 15. Böhm's Bee-eater (*Merops boehmi*); 16. Little Green Bee-eater (*Merops orientalis*).



considered more akin to small lowland forms of present species; further research required. Four subspecies currently recognized.

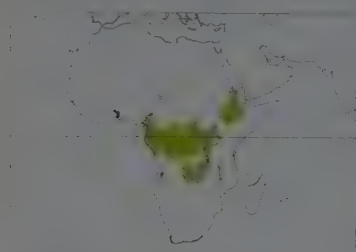
#### Subspecies and Distribution.

*M. v. loringi* (Mearns, 1915) - extreme SE Nigeria (Obudu and Mambilla Plateaux) and S Cameroon E to Uganda and W Kenya.

*M. v. variegatus* Vieillot, 1817 - Gabon E to SC Zaire (Kasai) and S to N Angola.

*M. v. bangweoloensis* (C. H. B. Grant, 1915) - C Angola, and Zambia W to W Tanzania.

*M. v. lafresnayii* Guérin-Méneville, 1843 - Ethiopia and SE Sudan.



**Descriptive notes.** 18-21 cm; 20-25 g. Nominative race has crown and upperparts green, a broad black eyestripe, white cheeks and neck sides, and yellow throat bordered below by deep purple-blue gorget with chestnut breast-band below that; rest of underparts light greenish-yellow to greenish-buff; secondaries pale rufous, primaries and secondaries tipped black; green tertials tend to wear or fade to bluish; tail rufous with black subterminal bar and white tip, central rectrices green; iris orange-red. Differs from *M. pusillus* in slightly larger size, and much more white bordering to cheeks; from *M. oreobates* in smaller size,

and more rufous, less green, on upper surfaces of secondaries and rectrices. Sexes alike. Juvenile lacks black gorget, has pale yellowish-buff chin and throat merging into light green breast and buff flanks and belly, breast mottled or streaked. Race *bangweoloensis* has black or bluish-black gorget, sometimes also very thin blue eyebrow; *loringi* similar, with more marked pale blue supercilium; montane race *lafresnayii* larger, with purple-blue gorget, blue forehead and eyebrow, rustier underparts and broader black bar in tail, altogether very like similar-sized, montane *M. oreobates*.

**Habitat.** In Ethiopia, *lafresnayii* inhabits lightly wooded steep slopes and, only on the plateau, grassy edges of coffee and eucalyptus plantations; occurs at 1000-3200 m. The other, lowland races prefer reedy lakeshores and papyrus beds, marshes, grassy hillsides, rank grassland at up to 2100 m, and forest glades. Broadly sympatric with *M. pusillus* in Ethiopia, Uganda, Rwanda, Zambia and Cameroon: where the 2 species occur in same area, present species found in open, permanently wet places and *M. pusillus* in drier ones with plenty of woody growth; on L. Victoria, 2 pairs inhabited a wet reedbed, open shrubby pasture and beaten-down sedges between reedbeds while, 100 m away, 2 pairs of *M. pusillus* selected dry pasture with small fields and thorn hedges; they may be interspecifically territorial.

**Food and Feeding.** Eats wide variety of airborne insects; in one study, 86% honeybees, flower bees, halictid bees, wasps and other Hymenoptera, 7% puprestid and other beetles, 5% flies, and 2% bugs, grasshoppers and damselflies; in another study, 19% honeybees, 33% other hymenopterans, 22% beetles, 16% flies, and 10% damselflies, dragonflies and grasshoppers. Foraging behaviour identical to that of *M. pusillus*, searching from perch, often in pairs, for passing insects and fly-catching or giving more or less horizontal chase; most prey taken within a few metres of perch. Exceptionally, plunge-dives into shallows for small fish.

**Breeding.** Breeds about Jan in Ethiopia, in Mar in Cameroon and N Zaire, Oct-Dec in Tanzania, Sept-Oct in Zambia. Nests solitary. Excavates tunnel in grassy hillside or small ridge in shelving ground near lakeshore; tunnel length 45-75 cm, ending in egg-chamber measuring 16.5-19.5 x 18-22 cm. Clutch of 2-3 eggs (Cameroon); no further details.

**Movements.** Mostly resident, though doubtless subject to same degree of local movements and nomadism induced by drying-out of marshy habitats as is *M. pusillus*. On Entebbe Peninsula, L. Victoria, found once to be common in Jul-Aug, but had disappeared by Sept.

**Status and Conservation.** Not globally threatened. Frequent to common in prime habitat in many parts of range. In Cameroon, common at 1900-2300 m on Mt Manenguba, less common at up to 2400 m on Mt Okur; annual burning of species territory in thick grassland by pastoralists there exposes bare earth and makes nesting habitat available, so local density may depend on continuation of stock-keeping. Present in several protected areas, e.g. Ruwenzori National Park (Uganda), Ruvuvu National Park (Burundi) and Gashaka-Gumti Reserve (Nigeria). Race *bangweoloensis* is very local.

**Bibliography.** Anon. (1998a, 1998b), Bannerman (1933, 1953), Benson (1945), Benson *et al.* (1971), Britton (1968, 1980), Britton & Harper (1969), Cave & Macdonald (1955), Chapin (1939), Christy & Clarke (1994), Dean (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgood *et al.* (1994), Friedmann (1930a), Friedmann & Williams (1969), Fry (1969b, 1973), Fry *et al.* (1988), Gartshore (1984), Hockey (1996), Jackson & Selator (1938), Jehl (1976), Lewis & Pomeroy (1989), Lippens & Wille (1976), Mackworth-Præd & Grant (1957, 1962, 1970), Nikolaus (1987), Olson, C. (1976), Pinto (1983), Serle (1950b), Shon *et al.* (1990), Sim (1979), Smith (1957), Snow (1978), Traylor (1963), Urban & Brown (1971), Zimmerman *et al.* (1996).

## 10. Cinnamon-chested Bee-eater

### *Merops oreobates*

**French:** Guépier montagnard **German:** Bergspint **Spanish:** Abejaruco Montano  
**Other names:** Cinnamon-breasted Bee-eater

**Taxonomy.** *Melitophagus oreobates* Sharpe, 1892, Mount Elgon.

Has been placed with other small, round-winged species lacking tail-streamers in genus *Melitophagus*, comprising present species and *M. muelleri*, *M. gularis*, *M. pusillus*, *M. variegatus*, *M. bullocki* and *M. bullockoides*. Sometimes regarded as forming a superspecies with *M. variegatus*; although some geographical overlap exists between them, they are segregated altitudinally. Race *lafresnayii* of *M. variegatus* often treated as conspecific with present species, but considered more akin to small lowland forms of that species; further research required. Monotypic.

**Distribution.** E African highlands: Sudan-Uganda border (Lolibat and Nangeya Mts); E Zaire (Lendu Plateau, and S to around Makungu region on W side of L. Tanganyika); SW Ugandan highlands S to Mahari Mt in W Tanzania; Mt Elgon on Uganda-Kenya border; and NC Kenya (Mts Kulal, Nyiru and Marsabit, Cherangani Hills, Maralal and Meru) and W & C Kenyan highlands S to N & E Tanzania (Crater Highlands, Kilimanjaro, Arusha National Park, Pare Mts, W Usambara and E Uluguru ranges). Reported sightings from S Ethiopia probably all refer to *M. variegatus lafresnayii*.

**Descriptive notes.** 21 cm; 25-29 g. Green above, with black mask; cheeks white, throat yellow; black pectoral band often bordered above by very narrow dark blue band, some birds with distinct purple wash over whole gorget patch; rusty-buff underparts; green tertials fade to bluish; tail green with black subterminal bar and white tip; iris red. Very similar to *M. variegatus*; best distinguished



**Food and Feeding.** Three studies in Kenya (near Nairobi) showed that diet consists overwhelmingly of honeybees (*Apis mellifera*); also eats other hymenopterans, butterflies, moths, beetles, flies and dragonflies. A sentinel feeder, perching 3-15 m up on side of tree or telephone wire in the open, making sorties after passing insects, and sailing back to knock insect's head and rub its tail (if a hymenopteran) against the perch.

**Breeding.** In C Kenya, some clutches in Feb-Apr but large majority in Oct-Jan, in and just after short rains; elsewhere in E Africa Dec-Mar. Inferred to be double-brooded near Nairobi, but proof still wanting; no other bee-eater known to be double-brooded. Colonial, usually 2-5 pairs within a few metres, once 10 pairs in 50-m road cutting; traditional cliff with 3 pairs may have 50 burrows, nearly all old ones. Adult helpers occur at some nests. Excavates burrow in earth cutting, quarry or high earthen cliff of stream at forest edge, always in vertical surface; burrow 60-70 cm long, inclining slightly and ending in offset brood-chamber 20 cm long, 15 cm wide and 7 cm high, with floor 4 cm below level of burrow. Clutch of 2 eggs in Kenya, 3 in Tanzania; incubation by both sexes, mainly by female, by day in half-hour spells with breaks of 5 minutes; nestling period 25 days or more.

**Movements.** Chiefly resident, but seasonal changes in abundance have been reported at a number of localities, and these are usually ascribed to local or altitudinal migration: in SW Kenya, for instance, species arrives at Mau Narok at 3000 m in Oct, breeds, and departs in Apr. Vagrant to S Somalia, once in May.

**Status and Conservation.** Not globally threatened. Status has not been monitored constantly enough for any long-term changes in population density to have emerged. While species nests in cliff sites in open country close to evergreen montane forest, it may prove to be sufficiently adaptable to withstand even widespread loss of forest habitat. Present in several protected areas, e.g. Bwindi Forest National Park (Uganda), Kibira National Park (Burundi), Kakamega Nature Reserve (Kenya) and Nyungwe Forest Reserve (Rwanda).

**Bibliography.** Bennun & Njoroge (1996, 1999), Betts (1966), Britton (1980), Brown & Britton (1980), Cave & Macdonald (1955), Chapin (1939), Dowsett (1990), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Friedmann & Stager (1967), Fry *et al.* (1988), Gerstner & Patzwahl (1987), Hockey (1996), Jackson & Selator (1938), Lewis & Pomeroy (1989), Lippens & Wille (1976), Loveridge (1928), Mackworth-Præd & Grant (1957, 1970), Nikolaus (1987), Prigogine (1971, 1978, 1984), Reynolds (1960), de Ruiter (1993b), Short *et al.* (1990), Snow (1978), van Someren (1956), Zimmerman *et al.* (1996).

## 11. Red-throated Bee-eater

### *Merops bullocki*

**French:** Guépier à gorge rouge **German:** Rotkehlspint **Spanish:** Abejaruco Gorgirrojo

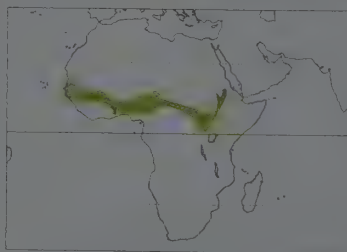
**Taxonomy.** *Merops Bulocki* [sic] Vieillot, 1817, Senegal.

Has been placed with other small, round-winged species lacking tail-streamers in genus *Melitophagus*, comprising present species and *M. muelleri*, *M. gularis*, *M. pusillus*, *M. variegatus*, *M. oreobates* and *M. bullockoides*. Forms a superspecies with *M. bullockoides*, with which sometimes treated as conspecific. A rare yellow-throated variant was first described as a separate species, *M. boleslavskii*. Species name sometimes emended to *bullocki*, but this is unjustified due to lack of internal evidence to this effect in initial description, so original spelling should stand. Two subspecies recognized.

#### Subspecies and Distribution.

*M. b. bullocki* Vieillot, 1817 - Senegal E to Central African Republic.

*M. b. frenatus* Hartlaub, 1854 - W Ethiopia, S Sudan, NE Zaire and NW Uganda.



**Descriptive notes.** 22 cm; 21-28 g. Green above, with deep buff hindneck and upper mantle; broad black eyestripe, scarlet throat; buff below, with blue lower belly and undertail-coverts; plumulaceous part of throat feathers grey, only pennaceous part scarlet. Barbs stiff, radiating and practically devoid of barbules; wings with black trailing edge; spread tail mainly ochreous, only tips of feathers and all of central pair green; mouth pink, iris dark brown, legs and feet dark grey. About 1% of N Nigerian birds have yellow throats; readily distinguished from other yellow-throated *Merops* species by blue undertail-coverts.

Sexes alike. Juvenile like adult, but red of throat and blue of flanks and undertail-coverts much less intense; broad green cheekstripe. Race *frenatus* differs from nominate in having pale blue forehead, eyebrow and cheek line.

**Habitat.** Bushy savanna dissected by small wooded rivers and seasonal streams; well-timbered gardens and farmland, edges of woods around fields and marshes, edges of gallery forest, parkland, *Combretum* scrub, and overgrazed and eroding pasture. Requires lateritic or hard-sand cliffs 2-5 m high for nesting, roosting and year-round socializing; generally uses cliffs by dry watercourses with gulleys erosion.

**Food and Feeding.** Diet at Zaria, Nigeria, is honeybees (*Apis*), varying from 5% in Jul-Aug to 45% in Mar-Jun; stingless bees taken abundantly in spring; also flying ants, a huge variety of other hymenopterans, and beetles, bugs, flies, dragonflies, damselflies, moths, butterflies, termites and grasshoppers. Insects fed to nestlings tend to be larger, weighing up to 0.6 g and on average 0.3 g. Airborne insects taken in short sallies from sentinel perch 2-5 m above soil; carries prey back to perch, where it is beaten and, if a bee, rubbed to de venom it; rarely, feeds in continuous flight aloft. A small proportion of birds do not themselves hunt, but wait at colony for other birds bringing food to mates or nestlings, and successfully kleptoparasitize them. Each



clan has a feeding territory up to 2 km from colony; clan-members fly to it together after dawn and defend it against non-clan birds.

**Breeding.** Burrows dug in Sept, before ground dries and hardens; eggs laid in Feb-Mar. Colonial, with usually 5-50 occupied burrows in colony, entrances often only 10 cm apart, covering cliff-face area of c. 1 m radius or arranged horizontally in low cliff. Breeding unit a pair or trio, sometimes 4 birds or more, including 2 or more helpers; helper is usually male of pair's offspring of a previous season, some are females or males whose breeding attempt has failed, usually close relatives of the pair; 2-4 breeding units form a clan, mainly of distant blood relatives. Obligate cliff-burrower, excavating in more or less vertical sandy, clayey or lateritic cliff by stream, in quarry, borrow-pit or road cutting through woodland, cliff 20 cm to 5 m high, usually 2 m. Pair and helpers dig burrow, generally among previous year's holes or in nearby cliff; entrance becomes A-shaped with use, the birds' feet wearing 2 channels; burrow 56-139 cm long, usually 80-85 cm, and 6 cm in diameter, inclining at 20° for two-thirds of length and, beyond a shallow hump in floor, expanding into brood-chamber 10 cm high, 20 cm long and 15 cm wide. Clutch of 1-5 eggs (mode 3); second egg laid 24 hours after first, third 1-2 days later; incubation begins with first or second egg, period 19-21 days, mainly by female by day but male and helper participate; all may roost in brood-chamber at night; clutches of 2, 3 and 4 eggs take 17, 43 and 72 hours, respectively, to hatch; nestling period c. 28 days. Clan-members visit each other's nest-burrows. Male spends much time guarding his mate to prevent extra-pair copulations, which nonetheless occur commonly, so pair often rears eggs other than its own.

**Movements.** In most regions strictly resident, birds remaining all year within few hundred metres of colony; partial migration or post-breeding dispersal along R Gambia, birds moving W in wet season, Jul-Oct. Single record from Sierra Leone, of small flock in Nov; only record in SE Nigeria was of flock of 20 flying N at Enugu in Jul.

**Status and Conservation.** Not globally threatened. Common, at least locally. In Nigeria, density near Zaria 260 breeding pairs in 25 km<sup>2</sup>, or 21 birds/km<sup>2</sup>, and in Yankari Game Reserve 25-50 birds/km<sup>2</sup> and 50-90 birds/km<sup>2</sup> in main river valley; extrapolation of Zaria value gives global total of 1,730,000 birds at start of breeding, and of lower Yankari value 2,000,000-4,000,000 birds. Present in several national parks, e.g. Niokola Koba (Senegal), Comoé (Ivory Coast), Kalamaloue and Benoue (Cameroon), Dinder (Sudan) and Kabalega Falls (Uganda).

**Bibliography.** Bannerman (1953), Barlow *et al.* (1997), Britton (1980), Carter & Robinson (1981), Cave & Macdonald (1955), Cheke & Walsh (1996), Crick (1984, 1986, 1987, 1993), Crick & Fry (1980, 1986), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dragasco (1960), Dyer (1975, 1979, 1983), Dyer & Fry (1980), Elgood *et al.* (1994), Fry (1966, 1967b, 1969a, 1969b, 1970a, 1972, 1973, 1977, 1983a), Fry & Crick (1980), Fry, Dyer & Crick (1984), Fry, Ferguson-Lees & Ash (1969), Fry, Keith & Urban (1988), Giraudoux *et al.* (1988), Gore (1990), Grimes (1987), Hockey (1996), Lippens & Wille (1976), Mackworth-Praed & Grant (1957, 1970), Nikolaus (1987), Short *et al.* (1990), Snow (1978), Walsh *et al.* (1990).

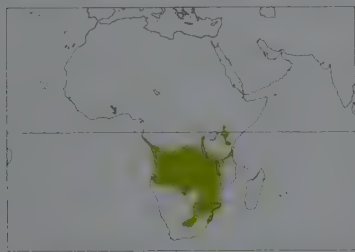
## 12. White-fronted Bee-eater

### *Merops bullockoides*

**French:** Guépier à front blanc **German:** Weißstirnsint **Spanish:** Abejaruco Frentiblanco

**Taxonomy.** *Merops Bullockoides* A. Smith, 1834, Marico district, Transvaal, South Africa. Has been placed with other small, round-winged species lacking tail-streamers in genus *Mellitophagus*, comprising present species and *M. muelleri*, *M. gularis*, *M. pusillus*, *M. variegatus*, *M. oreobates* and *M. bulocki*. Forms a superspecies with *M. bulocki*, with which sometimes treated as conspecific. Birds from S Tanzanian highlands sometimes separated as race *randonum*, but differences from other populations very slight. Species name has occasionally been listed as *bullockoides*, in apparent accordance with spelling of closely related *M. bulocki*, upon which original name of present species was presumably based; however, these details have no significance for scientific nomenclature, and original spelling must stand. Monotypic.

**Distribution.** W Gabon, NE Zaire (Virunga National Park) and NW Kenya (L Turkana) S to N & E Botswana, Orange Free State and Natal.



belly washed cinnamon. Differs from *M. bulocki* in white head markings, blue uppertail-coverts, bluer colour of back, wings and tail. Sexes alike. Juvenile like adult, but red of throat and blue of tail-coverts, flanks and vent less intense, whitish facial marks less strongly contrasting with adjacent colours.

**Habitat.** Broadleaf and mixed woodland along perennial rivers, dry watercourses in well-wooded country, eroded gulleys, scrub-covered stony hillsides, bushy pasture; in South Africa, associated with bee-attracting exotic trees such as eucalypts.

**Food and Feeding.** Hymenoptera form 87% of diet; also eats beetles, bugs, flies, dragonflies, damselflies, moths, butterflies, grasshoppers and cicadas. Hunts mainly from lower levels of trees and tall shrubs in bushy grassland; hawks with rapid dash out from perch and seizing or chasing insect, or makes slower, gliding flight down towards grass and low herbage and momentarily hovers to seize insect from it. Clan's foraging territory up to 7 km from breeding cliff, and clan-members space themselves out and hunt solitarily. Individual bird makes c. 300 sallies a day, nearly all to within 15 m of perch; good correlation of increasing prey size and capture rate with distance; overall success rate varies between 50% and 70%.

**Breeding.** In Kenya eggs laid in all months, mainly Oct-Feb, then Apr-Jun; Aug-Sept in Angola and Zambia; Aug-Nov in Zimbabwe and South Africa; pairs sometimes nest again 5-7 months after successful breeding. Birds' lives centred on traditional colony site throughout year, and society arguably the most complex and best-studied of any avian species; essentially monogamous, most pairs staying together for life, taking on helpers in some years or themselves helping to rear close relatives' young in others; during its lifetime, individual can change roles between breeding and helping several times; colonies generally of 10-20 nests attended by 30-80 birds, some of up to 450 birds; 60% of breeding pairs have 1-5 helpers, these being yearlings or experienced past breeders, which help with excavation, incubation, brood-feeding, and defence of nest

and feeding territory; 3-4 pairs with helpers comprise a clan, members of which are related and freely visit each other's burrows, but repel attempts by non-members to enter burrows; 2 populations studied at Nakuru, Kenya, comprised c. 400 birds in 60 clans at 100 active nests; males preponderate, and most helpers are male. Nests in riverbank cliff or erosion gully, excavated by all members of breeding unit; burrow 1-2 m long, ending in oval brood-chamber c. 20 cm long, 18 cm wide and 8 cm high. Males spend better part of day at colony, protecting female from enforced copulation by other males; 7% of all eggs in colony laid parasitically, parasitizing female spending much time observing neighbouring burrow-owners; to prevent being parasitized, female stays in her nest for most of daytime, removes any foreign egg before starting own clutch; considerable parent-offspring conflict, and parents may interfere in their son's nesting to recruit him as own helper. Clutch of 2-5 eggs, average 3-06 in helped nests and 2-54 in unhelped ones; growth rates of nestlings flexible, an adaptation to food shortage in bad weather; nestling survival greatly enhanced when brood attended by helpers as well as parents. Average longevity 5-6 years; small proportion of birds much longer-lived.

**Movements.** Generally resident; little evidence for any regular migrations, but seasonal variation in reporting rates in Zimbabwe and Transvaal, where commoner in Apr-Sept than Oct-Mar, and in S Africa often seen as partial migrant moving N after breeding; said to be passage migrant in Mar in C Shaba, Zaire. Vagrants near Namibian and S Cape coasts show that birds can wander great distances.

**Status and Conservation.** Not globally threatened. Common and widespread. Has benefited from human activities by nesting in quarries and cuttings; range thought to be extending along river valleys in N Cape and Orange Free State. Present in several national parks, e.g. Lake Nakuru (Kenya), Victoria Falls and Zambezi (Zimbabwe) and Kruger (South Africa).

**Bibliography.** Anon. (1995f, 1998b), Benson & Benson (1977), Benson *et al.* (1971), Britton (1980), Callegari (1956), Carter & Robinson (1981), Clancey (1953), Collett (1992), Cook & Cook (1994), Craig & Burman (1974), Dean (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Emlen (1979, 1981, 1982a, 1982b, 1982c, 1990), Emlen & Demong (1975, 1984), Emlen & Wrege (1986, 1988, 1989, 1991, 1992, 1994), Emlen, Demong & Hegner (1980), Emlen, Wrege & Demong (1995), Emlen, Wrege, Demong & Hegner (1991), Fitzgerald (1970), Fothergill (1988), Fry *et al.* (1988), Gee (1969), Ginn *et al.* (1989), Grobler & Joubert (1984), Harrison *et al.* (1997), Hegner (1981, 1982), Hegner & Emlen (1987), Hegner, Emlen & Demong (1982), Hegner, Emlen, Demong & Miller (1979), Herholdt & Earle (1987), Hockey (1996), Hume (1992), Koenig (1969), Lewis & Pomeroy (1989), Lippens & Wille (1976), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Martin (1999), Pagel (1995, 1997), Parker (1994), Penny (1994), Pinto (1983), Risley (1978), Short *et al.* (1990), Snow (1978), van Someren (1956), Steyn (1996b), Wrege & Emlen (1987, 1991, 1994), Zimmerman *et al.* (1996).

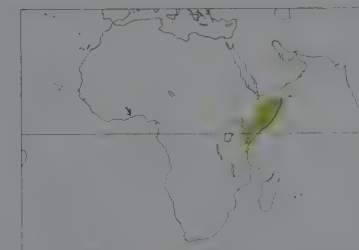
## 13. Somali Bee-eater

### *Merops revoilii*

**French:** Guépier de Revoil **German:** Somalispint **Spanish:** Abejaruco Somalí

**Taxonomy.** *Merops Revoilii* Oustalet, 1882, Somalia. Affinities within *Merops* by no means certain, but some evidence that it is closest to the *M. bulockii* *M. bullockoides* superspecies. Possibly a close relative of *M. albicollis*. Monotypic.

**Distribution.** Somalia, SE Ethiopia and N & E Kenya.



**Descriptive notes.** 16-18 cm; 12-15 g. The smallest bee-eater after *M. pusillus*; looks somewhat leggy, often adopting attenuated, heat-shedding stance with body high above perch and leg exposed nearly to "knee". Crown and back mealy greenish, glossy; nape and upper mantle buffy, rump azure-blue, quills dull blue-green; mask black, throat white, breast and belly fawn, undertail-coverts pale blue; forehead and crown feathers sharp-pointed, throat feathers thin and fluffy; plumage prone to abrade and fade to bluish; iris dark red-brown. Sexes alike. Juvenile plumage not described.

**Habitat.** Open *Acacia-Commiphora* thorn-scrub, arid steppe, grassland with scattered bushes and trees, thorn fences around cultivated fields, desert wells, coastal dunes, irrigated terraces, palmeries; also sometimes small clearings in impenetrable thickets.

**Food and Feeding.** Small airborne insects, captured in short sallies from bush.

**Breeding.** Breeds in Mar-Jun in Somalia and Kenya, and fledglings once seen in Oct. Poorly known solitary nester. Excavates burrow usually in earthen side of well or low road cutting; one in earth around roots of fallen palm was 60 cm long, straight, and declining.

**Movements.** Resident, but may move locally.

**Status and Conservation.** Not globally threatened. Very common in NW Somalia; widespread and quite common in SE Ethiopia, and in E Kenya locally common up to 1000 m and W to L Turkana. In SE Kenya, was not known S of R Galana until 1960's, but is now resident S to R Voi and has extended into Tsavo West National Park, with a sight record from NE Tanzania. Also present in Samburu and Marsabit Reserves (Kenya).

**Bibliography.** Archer, A.L. (1979), Archer, G.E. & Godman (1937-1961), Ash & Miskell (1983, 1998), Bennun & Njoroge (1999), Britton (1980), Brown & Britton (1980), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Friedmann (1930a), Fry *et al.* (1988), Hockey (1996), Leuthold (1973), Lewis & Pomeroy (1989), Mackworth-Praed & Grant (1957), Mann (1976), Short *et al.* (1990), Snow (1978), Urban & Brown (1971), Zimmerman *et al.* (1996).

## 14. White-throated Bee-eater

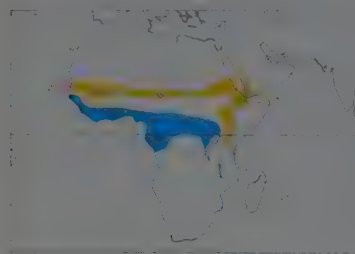
### *Merops albicollis*

**French:** Guépier à gorge blanche **German:** Weißkehlsint **Spanish:** Abejaruco Gorgiblanco  
**Other common names:** Black-crowned Bee-eater

**Taxonomy.** *Merops albicollis* Vieillot, 1817, Senegal. Has sometimes been placed together with *M. boehmi* in genus *Aerops*, as both species combine long outer primary with some characters of small *Mellitophagus* group (comprising *M. muelleri*, *M. gularis*, *M. pusillus*, *M. variegatus*, *M. oreobates*, *M. bulocki* and *M. bullockoides*) and with some features of large *Merops* species. Systematically rather isolated, with no obvious close relatives; possibly closest to *M. revoilii*. Separation of E populations as race *major* on grounds of longer bill and wings considered unwarranted. Monotypic.



**Distribution.** Breeds from Mauritania across to Yemen, and S to NW Kenya and, erratically, S Kenya; spends non-breeding season in W Africa and Congo Basin.



**Descriptive notes.** 20 cm (with streamers, up to 12 cm more); 20–32 g. Black crown and mask, contrasting with white face, even in juvenile; can raise crown feathers. Adult male has white head with black crown, eyeband and throatband; hindneck ochreous, back and wing-coverts green, rump and tail bluish; remiges mostly ochreous with wide black band on trailing edge; breast very pale green, of shade rare in birds, belly white; iris dull crimson to bright red. Female as male but streamers shorter, up to 8.5 cm; tends to have narrower black gorget and less pure black mask. Juvenile like adult, but green parts more

olive; breast and tertials olive-green; central pair of rectrices barely longer than others, dull green-blue, with oval black patch near ends; chin and throat pale yellow; all dark contour feathers narrowly pale-tipped, giving scalloped appearance.

**Habitat.** Breeds in very sparsely wooded subdesert steppe, sandy wastes, wadis, laghs and arid thorn-scrub; winters in large clearings in equatorial and W African forest, and in savanna woodland, orchard-bush, farmland and large suburban gardens, also mangroves.

**Food and Feeding.** Ants make up 35–90% of diet; also eats honeybees (*Apis*), other hymenopterans, beetles, bugs, flies, dragonflies, damselflies, grasshoppers, butterflies and ant-lions (Myrmeleonidae); occasionally takes small lizards from ground. A sortie feeder that tends to make longer forays than other fly-catching bee-eaters; also feeds in continuous flight on airborne ants and some termites, and takes some insects from ground; catches and eats strips of fruits of oil palms (*Elaeis guineensis*) dropped by squirrels (*Funisciurus*) and weavers (*Ploceus*) feeding in palm crown (see page 312). In winter, hawks from tops of largest emergent trees in primary forest.

**Breeding.** Breeds over ephemeral rains in Jun-Aug on borders of Sahara; in Mar-May in Kenya. Nests solitarily or in small, loose colonies; in locality in Mauritania 250 nests year after year. Nearly all pairs have helpers, usually 1, often 2–3, sometimes 4–5; helpers assist in all nest duties. The only bee-eater with distinctive aerial courtship flight, alternately gliding with wings high and flapping, with loud calling. Excavates burrow in flat or shelving sand, often in lee of tussock, stick or large-mammal dropping; burrow 1–2 m long, straight, declines at c. 23°, with egg-chamber at end angled horizontally to one side and with floor 38–58 cm below flat ground level. Clutch of 4–7 eggs, usually 5 or 6.

**Movements.** A long-distance intra-tropical migrant, travelling in noisy flocks by day, conspicuously, and seen with much regularity and predictability at many stations between Saharan nesting grounds and rainforest zone. Non-breeders present in Sierra Leone late Oct-early Jun. Lays down fat just before departure from non-breeding grounds, weight increasing by 15%; visitors to Yemen probably cross Gulf of Aden. Those spending non-breeding season in Cabinda (N Angola) and SW Congo make return journey of at least 2200 km if to L Chad, or c. 3000 km if to Sudan. More or less resident near equator in E Africa. Vagrant to South Africa.

**Status and Conservation.** Not globally threatened. Common over most of breeding range, and frequent or locally abundant in derived savanna and above rainforest outside breeding season. Little known about demographic structure, but evident high productivity should counterbalance known high mortality on breeding grounds, where many birds die in sandstorms and drought conditions. Present in numerous national parks, e.g. Taï Forest and Maroué (Ivory Coast), Mount Kupé, Benoue and Dja (Cameroon), Air et Ténéré (Niger) and Ruwenzori (Uganda); also in Gola Forests Reserves (Sierra Leone), Ouadi Rime-Ouadi Achim Reserve (Chad) and Kakamega Nature Reserve (Kenya).

**Bibliography.** Archer & Godman (1937–1961), Ash & Miskell (1998), Aspinwall (1992b), Bannerman (1933, 1953), Barlow *et al.* (1997), Britton (1980), Cave & Macdonald (1955), Chapin (1939), Cheke & Walsh (1996), Christy & Clarke (1994), Colston & Curry-Lindahl (1986), Coulthard (1988), Cunningham-van Someren (1970), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dowsett *et al.* (1999), Dowsett-Lemaire *et al.* (1993), Dyer & Crick (1983), Elgood, Fry & Dowsett (1973), Elgood, Heigham *et al.* (1994), Evans, M.I. (1994), Friedmann (1930a), Fry (1964, 1966, 1967a), Fry *et al.* (1988), Gass (1963), Gatter (1997), Giraudoux *et al.* (1988), Grimes (1987), Hockey (1996), Hopson & Hopson (1977), Jennings (1995), Lamareche (1980), Lewis & Pomeroy (1989), Lippens & Wille (1976), Mackworth-Præd & Grant (1957, 1962, 1970), Newby (1980), Nikolaus (1987), Perry (1989), Petit (1969), Pinto (1983), Porter *et al.* (1996), Reynolds (1974), de Ruiter (1993b), Short *et al.* (1990), Smith (1955), Snow (1978), Thiollay (1970, 1973b), Traylor (1963), Vaurie (1959), Zimmerman *et al.* (1996).

## 15. Böhm's Bee-eater

### *Merops boehmi*

**French:** Guépier de Böhm

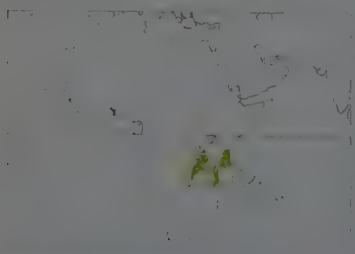
**German:** Böhmspint

**Spanish:** Abejaruco de Boehm

**Taxonomy.** *Merops (Melittophagus) boehmi* Reichenow, 1882, Bumi, Tanzania.

Has sometimes been placed together with *M. albicollis* in genus *Aerops*, as both species combine long outer primary with some characters of small *Melittophagus* group (comprising *M. muelleri*, *M. gularis*, *M. pusillus*, *M. variegatus*, *M. oreobates*, *M. bulcocki* and *M. bulcockoides*) and with some features of large *Merops* species. A somewhat enigmatic species, doubtfully allied with *M. orientalis*. Monotypic.

**Distribution.** SE Zaire, SW Tanzania and Zambia, with disjunct population in E Tanzania and Malawi and adjacently in Mozambique.



**Descriptive notes.** 16 cm (with streamers, up to 7 cm more); 17–20 g. A smallish, rather elegant green bee-eater with cinnamon crown, and rich ochreous throat without dark gorget line; shows broad black eyestripe and very narrow blue cheekline; also has indistinct thin blackish line along trailing edge of wing, and distinct black tip to tail except on the central feathers, which are markedly streamered and are also club-tipped; wingtip rather rounded; iris crimson. Sexes very similar, but female has shorter tail. Juvenile similar to adult, more so than in any other bee-eater species, but shows less ochre on throat and central

rectrices are not elongated.

**Habitat.** Glades and rides in park-like woodland with large shade trees separated by patches of short grass sward; also thorny scrub, thickets, riparian forest, burnt-over ground, and small hedged and wooded fields.

**Food and Feeding.** Eats honeybees (*Apis*) and many other hymenopterans, beetles, grasshoppers, butterflies, cicadas, bugs and many flies. Feeds by hawking in short forays from perch in dappled shade 2–3 m above ground, giving chase to passing insect 5–12 m from perch; perches on twigs but not on grass stems. Bouts of active feeding alternate with long periods of inactivity.

**Breeding.** Eggs laid in Sept-Oct. Solitary or in small loose colonies; sometimes 2–4 pairs nest within 20 m of each other. Pair excavates nest-burrow in level, part-shaded, well-drained ground by footpath or sandy clearing; burrow straight, declining gently, 75–100 cm long. Clutch of 2–4 eggs; incubation and nestling periods unknown.

**Movements.** Resident.

**Status and Conservation.** Not globally threatened. In general scarce, and unaccountably absent from many areas that look suitable; plentiful around L. Suze, in Zaire; uncommon and distinctly local in Zambia, although in 1930's was found to be the commonest bee-eater around Ndola. Fairly common though very local in Shire Valley, S Malawi, where thought to be 100's of pairs in only a small part of Lengwe National Park, and is noticeably more abundant in Liwonde National Park, where seems to be on the increase in a sugar-estate housing area. In Mozambique, 12 groups of 2–5 birds counted within 4-km radius of Mopeia. Species appears to be commonest in undisturbed natural parkland; it would almost certainly suffer if large areas were entirely cleared of woody growth for agriculture, but seems to be holding its own where plenty of shrubby, disturbed woodland remains. Present in several national parks, e.g. Mikumi (Tanzania), Kafue (Zambia) and Liwonde and Lengwe (Malawi).

**Bibliography.** Bennun & Njoroge (1996), Benson & Benson (1977), Benson & Pitman (1959), Benson *et al.* (1971), Britton (1980), Chapin (1939), Clancey (1985, 1996), Dowsett & Dowsett-Lemaire (1979, 1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Ginn *et al.* (1989), Hamner (1980a), Hockey (1996), Irwin & Benson (1967), Lippens & Wille (1976), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Short *et al.* (1990), Snow (1978).

## 16. Little Green Bee-eater

### *Merops orientalis*

**French:** Guépier d'Orient

**German:** Smaragdspint

**Spanish:** Abejaruco Esmeralda

**Other common names:** Least/Small Green Bee-eater

**Taxonomy.** *Merops orientalis* Latham, 1801, Mahratta, India.

Relationships uncertain; no obvious close relatives, and affiliations with *M. boehmi* doubtful. Races fall into three well-defined geographical groups: African *viridissimus*, *flavoviridis* and *cleopatra*; Arabian *cyanophrys* and *muscatensis*; and Asian *beluschicus*, *orientalis* and *ferrugineiceps*. Arabian group is the most distinctive and might well be regarded as a species in its own right; in that event, a superspecies of three, namely *M. viridissimus*, *M. cyanophrys* and *M. orientalis*, could be recognized. Race *flavoviridis* perhaps invalid, as different throat colour thought possibly result of plumage being very fresh or, alternatively, worn. Proposed race *nadjanus* now included within *muscatensis*; *birmanus* is synonym of *ferrugineiceps*. Eight subspecies currently recognized.

**Subspecies and Distribution.**

*M. o. viridissimus* Swainson, 1837 - Senegal across to N & C Ethiopia.

*M. o. flavoviridis* Niethammer, 1955 - NE Chad (Ennedi) E to Red Sea coast in Sudan.

*M. o. cleopatra* Nicoll, 1910 - Nile Valley S to N Sudan.

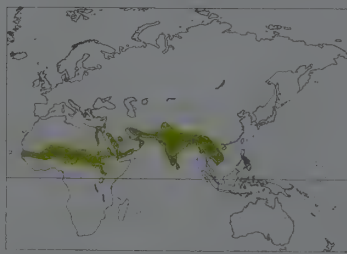
*M. o. cyanophrys* (Cabanis & Heine, 1860) - S Israel, and W & S Arabian coasts.

*M. o. muscatensis* Sharpe, 1886 - C Arabian plateau and E Arabia.

*M. o. beluschicus* Neumann, 1910 - S Iraq E to NW India (W Rajasthan).

*M. o. orientalis* Latham, 1801 - W India (Rann of Kachchh) E to Bangladesh and S to Sri Lanka.

*M. o. ferrugineiceps* J. Anderson, 1878 - NE India (E Assam) and SC China (Yunnan) to Vietnam.



**Descriptive notes.** 16–18 cm (with streamers, up to 10 cm more); 15–20 g. A small but long-tailed bee-eater, geographically highly variable. Nominata race mostly bronzy green, with golden-green crown and hindneck, black band through eye, blue cheeks, pale bluish-green chin and throat, thin black gorget, black trailing edge on wing; underside of tail shiny grey; tail-streamers long, up to c. 7 cm; iris crimson. Female like male, but streamers average shorter; tends to have duller throat and narrower gorget. Juvenile like adult, but pallid, lacks black gorget, body with barely discernible scalloped appearance, mask dusky

rather than black, breast pale green, belly almost white; at first appearance gorget may be transitorily blue rather than black; occasional juveniles of all races have yellow or yellowish-green throat. Races vary greatly in colours of throat, crown and nape, width of gorget, and length and degree of attenuation of streamers: *viridissimus* has crown, hindneck and throat grass-green, very long streamers, up to c. 10 cm; *flavoviridis* virtually identical to *viridissimus*, but throat can be yellow instead of green, perhaps dependent on plumage state; *cleopatra* less bronzy than nominate, long streamers up to 8.5 cm; *cyanophrys* has greens less bronzy, more blue-tinged, forehead, eyebrow and throat blue, gorget deep and less well defined, streamers short and pointed, up to c. 2 cm; *muscatensis* like previous but generally more yellow-green, and shows narrower gorget; *beluschicus* has golden-green crown and nape, pale blue chin becoming pale green on lower throat, gorget a very narrow line, streamers up to 6 cm; *ferrugineiceps* shows rufous crown, nape and mantle, mask often narrowly bordered with green line above and pale blue below, green throat, streamers up to 6 cm.

**Habitat.** Arid woodland with scattered trees on mainly bare soil or sand, and *Acacia*, *Commiphora* and *Leptadenia* woodland with grassy undercover; also date-palm groves, wadis, thickets and thorn hedges around crops, lakesides, overgrazed pasture with thickets of *Salvadora* or *Lantana*, plantations, spacious gardens, dunes and farmland. Occurs from sea-level up to c. 2000 m in India, though only to c. 1250 m in Africa.

**Food and Feeding.** Feeds mainly on Hymenoptera, also beetles, termites, bugs, moths and many flies, ranging in size from fruit-flies (*Drosophila*) to large elegs; also a few butterflies, crickets, dragonflies, spiders and caterpillars. Hymenoptera comprise 75% of diet in Africa; eats many honeybees, including *Apis cerana* in Pakistan. *A. florea* in India and the large *A. dorsata* in Myanmar. Hunts from perch on fence, small thorny tree or sometimes the back of grazing cattle or antelope, making sallies low over vegetation.



**Breeding.** Throughout range eggs laid in Mar-Jun, occasionally also in Jul-Aug. Breeds solitarily in Africa and Arabia, in loose colonies with nests 10-100 m apart in India, and in dense colonies of 10-30 pairs in Pakistan and Myanmar; helpers have not been reported. Nest-burrow dug by both sexes, into flat or gently sloping ground in Africa or often into low bank or cutting in Asia; burrow up to 1 m long in hard soil and 2 m long in soft soil, declines by 20°-30° and is 5-6 cm wide, with terminal egg-chamber 15 cm long, 12 cm wide and 9 cm high. Clutch of 4-8 eggs, usually 6; female incubates more than male; incubation and nestling periods unknown; both sexes provide for the young.

**Movements.** Resident and partial migrant in Africa, rather more migratory in Asia. In W Africa, post-breeding dispersal to N causes influx during later part of nesting season, about Jun-Aug, near N limits of range. Generally resident and dispersive in Israel and Egypt, and tends to move S up R Nile for winter; scarce non-breeding visitor to N Uganda and N Kenya. Much commoner in N Oman in winter than in summer, attributable to migration from Iran or perhaps Pakistan. Markedly seasonal in Indian Subcontinent, withdrawing from N in winter and from wet areas in monsoon season; also subject to some altitudinal movements.

**Status and Conservation.** Not globally threatened. Locally common to fairly common over whole of vast range. In earlier 20th century, species expanded N in Egypt, into lower Nile Valley and to

Nile Delta; during 1960's and 1970's it invaded new areas in Arava Valley, Israel, following agricultural development, and later spread N into Dead Sea Depression; in 1987, c. 300 breeding pairs in Israel. Present in numerous national parks throughout wide range, e.g. Niokola Koba (Senegal), Waza (Cameroon), Khirthar (Pakistan), Chitwan (Nepal), Bharatpur (India), Uda Walawe and Yala (Sri Lanka) and Khao Sam Roi Yot (Thailand).

**Bibliography.** Ali (1996), Ali & Ripley (1983), Aspinall (1996), Baker (1934b), Bannerman (1953), Barlow *et al.* (1997), Bastawde (1976), Beaman & Madge (1998), Cave & Macdonald (1955), Cramp (1985), Deiguan (1945), Dereniyagala (1956), Dhindsa & Saini (1991), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Duckworth *et al.* (1999), Elgood *et al.* (1994), Étiéhopar & Hue (1964, 1978), Evans, M.J. (1994), Fry (1975a), Fry *et al.* (1988), Giraudoux *et al.* (1988), Goodman *et al.* (1989), Gore (1990), Grimmett *et al.* (1998), Henry (1998), Hockey (1996), Huda (1997), Hue & Étiéhopar (1970), Inskipp, C. & Inskipp (1991), Inskipp, T. *et al.* (1996), Jennings (1981a, 1990, 1995), Latif & Yunus (1950), Lekagul & Round (1991), MacKinnon & Philipps (2000), Mackworth-Praed & Grant (1957, 1970), Madge (1981), Mason & LeFroy (1912), McClure (1998), Meyer de Schauensee (1984), Mishra & Kaushik (1993), Moreau (1927), Mukherjee (1995), Nikolaus (1987), O'Brien (1922), Paz (1987), Phillips (1978), Porter *et al.* (1996), Ripley (1982), Roberts (1991), Robson (2000a), Round (1988), Shirahai (1996), Short & Horne (1981), Smythies (1986), Snow (1978), Snow & Perrins (1998), Sugathan & Varghese (1996), Ticehurst *et al.* (1922), Vaurie (1959), Yang Lan *et al.* (1995), Zhao Zhengjie (1995).

*ssp persicus*

17

*ssp chrysocercus*

*ssp superciliosus*

18

green-crowned bird

*ssp alternans*

normal bird

*ssp americanus*

21

*ssp viridis*

19

20

*ssp leschenaulti*

22

*ssp quinticolor*

*ssp andamanensis*

23

24

*ssp nubicoides*

25

*ssp nubicus*



# 17. Blue-cheeked Bee-eater

## *Merops persicus*

French: Guépier de Perse

German: Blauwangenspint

Spanish: Abejaruco Persa

**Taxonomy.** *Merops persica* Pallas, 1773, shores of the Caspian Sea.

Forms a superspecies with *M. superciliosus* and *M. philippinus*, and the three taxa have often been regarded as conspecific. Present species, however, shows striking plumage differences from *M. superciliosus*, and breeds sympatrically with *M. philippinus* in N Pakistan and India; in some regards, those two species are more similar to each other than either is to present species. Two subspecies recognized.

### Subspecies and Distribution.

*M. p. chrysocercus* Cabanis & Heine, 1860 - borders of W Sahara, from Morocco to Algeria and from Senegal patchily to L Chad; winters in sub-Saharan W Africa.

*M. p. persicus* Pallas, 1773 - Egypt (Nile Delta), N Israel (irregular) and SE Turkey, S to Persian Gulf, and E to N shores of Caspian and Aral Seas, S shores of L Balkhash, N Afghanistan (Hindu Kush) and N & W India (Delhi and Gujarat); winters mainly in E tropical Africa.

**Descriptive notes.** 31 cm (with streamers, up to 7 cm more); 38-56 g. A large, slim bee-eater with long wings. Male of nominate race with upperparts grass-green in fresh plumage, wings and tail more golden-green, sometimes all parts except rump quite strongly olive; with bleaching or wear turns more bluish, particularly on tertials and rump; wings with narrow, dusky trailing edge; forehead narrowly white by bill, shading backwards to powder-blue, but often, possibly immature birds, forehead yellowish and blue eyebrow poorly developed; broad black eyeband; cheeks broadly blue but may be narrowly white; chin bright yellow, sometimes dull yellow; throat rufous, underparts bright green; axillaries and entire underwing except distal halves of flight-feathers russet; bill long and slender, black; iris claret. Distinguished from *M. superciliosus* by green crown, presence of blue and yellow colours, lack of white surround to bill and mask; rather more similar to *M. philippinus*, from which differs in rump and tail being green, not blue, and moustachial area being green, not rufous-brown. Female like male, but tail-streamers average shorter, iris orange-red. Juvenile olive-green above except for blue-green rump and ochre tinge on head; nape and body markedly scaly, feathers narrowly white-fringed; forehead narrowly buffy, eyebrow yellowish-buff; chin pale buff, washed yellow; throat warm buff, yellowish or white towards cheeks; breast pale green, scaly; undertail-coverts very pale green; moults directly into adult plumage 4-5 weeks after fledging. Race *chrysocercus* has upperparts more golden, and is slightly smaller than nominate, though streamers often longer.

**Habitat.** In summer, occupies desert, semi-desert, steppe, dunes, saline pans, cultivation, thorn woodland and sandy slopes with small gulleys, ravines, quarries, pits and embankments; breeds mainly in sand deserts near bodies of water fringed with reeds and tamarisks. In Africa during non-breeding season, inhabits a wide variety of greener habitats: savanna, broad river valleys, woods, lakeshores, swamps, ponds, dams, waterworks and cultivation; flocks roost in mangroves in Sierra Leone.

**Food and Feeding.** Eats mainly hymenopterans on Asian breeding grounds and mainly dragonflies in Africa; many dragonflies also taken in Asia, on average constituting only c. 15% of diet, but in some places predominating. Takes much greater diversity of airborne insects even than does, e.g., *M. apiaster*; almost exclusively honeybees (*Apis*) when they are plentiful; catches very small insects as well as large beetles, locusts and cicadas. Feeds by making long pursuit-flights from telephone wires, fences, treetops, even from ground; makes height with fast, even wingbeats, glides, then twists abruptly after its prey; some wasps are seized from below, with bird's head thrown back and its bill pointing straight up. Returns to perch to knock prey and, if hymenopterans, to rub its tail. Often forages in continuous flight; occasionally follows moving vehicle to catch insects dislodged from grass.

**Breeding.** Eggs laid in Mar-Jun, but in any one region all birds lay within 3 weeks of each other. Monogamous; helpers at nest not certainly recorded. Nests solitary, or more commonly in loose colonies of c. 10 in 1 ha; often forms mixed colonies with *M. apiaster*. Sited in bank of canal or irrigation ditch, seashore (Caspian), low cliff of compacted, wind-scoured sand dune, hard-baked sandy mud plain or large, enclosed pasture, also in earthen shoulder of metalled road, burrow then extending beneath tarmac; excavates in level, sandy ground, slope, declivity face or cliff, always in cliff when mixed with *M. apiaster*; burrow 1-3 m long depending on softness of soil, nearly straight, in cliff horizontal and in level ground declining at c. 20°, entrance 7.5-8.5 cm wide, 5-7.5 cm high, with terminal egg-chamber 15-20 cm long, 9 cm wide and 12 cm high. Clutch of 4-8 eggs, usually 6-7; incubated by both parents by day, by female alone at night; incubation period 23-26 days and nestling period c. 30 days, neither known well and hard to measure, as laying, hatching and young fledging all asynchronous.

**Movements.** A long-distance migrant, moving in small and large flocks, mainly by day, passing on broad front often at considerable height; vacates breeding grounds in Aug, arrives in non-breeding quarters from Nov. On long sea crossings obliged to migrate at night; at Karachi, S Pakistan, spring migrants cross during 5 hours in middle of night. Sometimes migrates with *M. apiaster*, but in spring tends to arrive on breeding grounds 2 weeks later than that species. Saharan population winters in sub-Saharan W Africa; occurs all winter around L Chad, and still present on reed islands far out into the lake in mid-Jul. Asian population winters partly in India, Pakistan and Yemen, but mainly in E half of Africa from Ethiopia to NE Namibia, Botswana, W Transvaal and NE Natal; most enter Africa along Nile Valley and across Red Sea, where many killed by Sooty Falcons (*Falco concolor*).

**Status and Conservation.** Not globally threatened. Generally rather common and widespread, and not known to be unduly threatened on breeding or non-breeding grounds. Colonies near human habitation are often mindlessly harassed by people; flat-ground colonies can be obliterated, or the birds forced to move away locally, by agricultural developments; yet even on the intensively settled and cultivated Batinah coast of N Oman, for instance, the species seems to be holding its own. Present in several protected areas, e.g. Khirthar National Park (Pakistan) and Mian Kaley Wildlife Refuge (Iran).

**Bibliography.** Adamian & Klem (1999), Ali & Ripley (1983), Anon. (1998b), Archer & Godman (1937-1961), Ash & Miskell (1998), Aspinall (1996), Aspinwall & Hustler (1997), Bannerman (1953), Barlow *et al.* (1997), Bates (1934), Baumung (1995), Beaman (1994), Beaman & Madge (1998), Belousov & Kossenko (1992), Benson *et al.* (1971), Borrett (1973), Bundy (1976), Cave & Macdonald (1955), Clapham (1964), Cramp (1985), Dementiev & Gladkov (1951), Dharmakumarsinhji (1947), Dolgushin *et al.* (1960-1972), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dyer (1980), Eates (1939), Ebels & van der Laan (1994, 1995), Elgood, Fry & Dowsett (1973), Elgood, Heigham *et al.* (1994), Esmaili (1974), Étchécopar & Hue (1964), Evans, M.I. (1994), Fry (1970b, 1981a, 1981b, 1992), Fry, Eriksen & Al-Ariny (1994), Fry, Keith & Urban (1988), Gatter (1997), Ginn *et al.* (1989), Glutz von Blotzheim & Bauer (1980), Goodman *et al.* (1989), Gore (1990), Grimes (1987), Grimmett *et al.* (1998), Hagemeijer & Blair (1997), Handrinos & Akriotis (1997), Hamner (1980a), Harrison *et al.* (1997), Hartley (1966), Hazevoet (1996a), Himmatninhji (1981), Hockey (1996), Holmes (1972), Holmes & Wright (1968-1969), Hue & Étchécopar (1970), Hutson (1947), Inskipp *et al.* (1996), Jennings (1995), Khacher (1975), Koenig (1953, 1956), Kossenko (1992, 1994a, 1994b, 1994c), Kossenko & Fry (1998), Kumerloeve (1968, 1972), Larsen (1992), Larsen *et al.* (1991), Lewis & Pomeroy (1989), Lippens & Wille (1976), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Marchant (1963), Marien (1950), Meinertzhagen (1954), Moreau (1972), Mukherjee (1995), Parslow (1972), Paz (1987), Pinto (1983), Porter *et al.* (1996), Ripley (1982), Roberts (1991), Sagitov & Fundukchiev (1980), Salvan (1968), Savin & Gistsov (1983), Shirihai (1996), Snow (1978), Snow & Perrins (1998), Stepanyan (1990), Ticehurst *et al.* (1922), Violani (1986), Vuilleumier (1977), Walsh (1968), Zimmerman *et al.* (1996).

# 18. Olive Bee-eater

## *Merops superciliosus*

French: Guépier de Madagascar

German: Madagaskarspint

Spanish: Abejaruco Malgache

Other common names: Madagascar/Malagasy/Brown-breasted Bee-eater

**Taxonomy.** *Merops superciliosus* Linnaeus, 1766, Madagascar.

Forms a superspecies with *M. persicus* and *M. philippinus*, and the three taxa have often been regarded as conspecific. Perhaps more closely related to *M. philippinus*, with which still frequently treated as conspecific, but differs significantly in some plumage characters: shows striking plumage differences from *M. persicus*. Two subspecies recognized.

### Subspecies and Distribution.

*M. s. superciliosus* Linnaeus, 1766 - E Ethiopia, Somalia and E Kenya to NE Tanzania and S Mozambique; also Comoro Is and Madagascar; sporadically in NW Zimbabwe.

*M. s. alternans* Clancey, 1971 - W Angola and NW Namibia.

**Descriptive notes.** 31 cm (with streamers, up to 7 cm more); 40-48 g. General plumage olive-green; crown dark olive-brown, forehead and supercilia white, mask black with broad white band below, chin yellowish-white, throat rufous-tan; axillaries and underwing-coverts ochreous; iris claret; mouth pale pink. Distinguished from *M. persicus* by olive-green rather than grass-green plumage, dark olive-brown cap, broader tan throat patch, and black mask and base of bill surrounded by white, also by ochreous rather than cinnamon axillaries and underwing-coverts; from *M. philippinus* by green rump and tail, white

around mask, darker olive crown. Female like male but streamers shorter, up to 5-3 cm. Juvenile duller, very like that of *M. philippinus*. Race *alternans* brighter green, crown often fully green, chin and cheeks whiter.

**Habitat.** Occurs in riverine woodland and open country up to 1500 m in Madagascar, hunting also over stands of heavy forest; eroded country, plantations, woodland, cultivation and open beaches in Comoro Is. In Africa, small offshore islands in Mozambique, mangroves, tree-lined beaches, suburban gardens; disturbed scrub and open country away from water in Malawi; swamps, and grassland with scattered *Acacia*, and *Acacia-Commiphora-Chrysopogon* stands in steppe country elsewhere.

**Food and Feeding.** Not so well studied as *M. persicus* or *M. philippinus*, but from all accounts foraging methods and diet both very similar to those: hymenopterans and a variety of other small and large insects, taken in wheeling sortie flights and continuous feeding on the wing.

**Breeding.** Eggs laid in Sept-Nov in Madagascar, in Nov in Comoros, in Sept-Dec in Namibia, Zimbabwe and Mozambique, about May-Aug in Tanzania (Zanzibar, Mafia I, Momela Crater L.), and in Apr-May and Nov-Dec in Kenya, Ethiopia and Somalia. Nests are isolated, or in colonies of tens or hundreds. Pair excavates burrow in riverbank, road cutting, earthen side of a field well, or sometimes in level, sandy ground; one burrow 175 cm long, ending in chamber 30 cm below soil surface, others 1-2 m long. Clutch of 4-6 eggs. Few further details of breeding known.

**Movements.** Apparently resident in Madagascar, and probably also in Comoro Is; migration between Madagascar and African mainland alleged, but no convincing evidence. In Africa, variously resident, partially migratory or a breeding or non-breeding visitor: resident in NW Somalia, and in Kenya a non-breeding migrant (May-Sept, Nov-Mar) and an erratically breeding resident near coast; a breeding visitor to SW Angola and NW Namibia in Sept-Jun (commonest in Nov-Apr), and a non-breeding visitor to Mozambique littoral, sometimes breeding S to N Natal, in Sept-Apr.

**Status and Conservation.** Not globally threatened. Widespread and generally common in Madagascar; a locally abundant breeder in NW Somalia and SW Angola, and seasonally widespread and common or locally numerous on wintering grounds in NE Zaire and along E and SE African seaboard. In Tsavo East National Park, Kenya, 2-3 birds/ha. Also present in Awash National Park (Ethiopia).

**Bibliography.** Anon. (1998b), Archer & Godman (1937-1961), Ash & Miskell (1998), Aspinwall & Hustler (1997), Benson (1960), Benson & Benson (1977), Benson, Brooke *et al.* (1971), Benson, Colebrook-Robjent & Williams (1976-1977), Britton (1980), Brooke & Hougard (1971), Bullock & Bullock (1976), Chapin (1939), Clancey (1971b, 1996), Dean (2000), Dean & Brooke (1991), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry (1981a, 1981c), Fry *et al.* (1988), Ginn *et al.* (1989), Harrison *et al.* (1997), Hartley (1986), Hockey (1996), Irwin (1981), Kruger (1990), Lack (1985), Langrand (1995a), Lewis & Pomeroy (1989), Lippens & Wille (1976), Louette (1988a), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Milton *et al.* (1973), Pakenham (1979), Pinto (1983), Rand (1936), Short *et al.* (1990), Snow (1978), Took (1963), Traylor (1963), Urban & Brown (1971), Zimmerman *et al.* (1996).

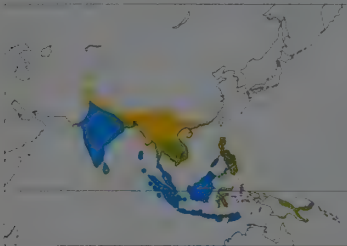


## 19. Blue-tailed Bee-eater

*Merops philippinus***French:** Guépier à queue d'azur **German:** Blauschwanzspint **Spanish:** Abejaruco Coliazul**Taxonomy.** *Merops philippinus* Linnaeus, 1766, Philippines.

Forms a superspecies with *M. persicus* and *M. superciliosus*, and the three taxa have often been regarded as conspecific. Present species, however, breeds sympatrically with *M. persicus* in N Pakistan and India; perhaps more closely related to *M. superciliosus*, with which still often treated as conspecific, but shows significant plumage differences. On grounds of coloration, birds of Sulawesi have been awarded race *celebensis* and those of E New Guinea and Bismarck Archipelago race *salvadorii*, with the nominate race restricted to the Philippines and all the remainder of the range being attributed to race *javanicus*; however, differences in hue only very slight. Monotypic.

**Distribution.** N Pakistan, India, Nepal and SE Sri Lanka E to Myanmar, SE China (Yunnan to Guangdong and Hainan) and Philippines, and S to Sulawesi and Flores; also E New Guinea and New Britain.



**Descriptive notes.** 29 cm (with streamers, up to 7 cm more); 29–43 g. Green above, with blue rump and tail; broad black eyestripe, bordered with narrow blue streak below, usually very thin blue line above; chin yellow, throat and cheeks rufous-tan; underparts green, undertail-coverts blue; iris claret. Differs from rather similar *M. persicus* in having lower half of cheek and moustachial area same tan colour as throat, not green, and rump and tail blue, not green; from *M. superciliosus* in greener crown, blue rump and tail, blue stripe below mask. Sexes alike. Juvenile duller and bluer, head and body with white feather fringes, chin

yellow-buff, throat rufous-buff, very like juvenile *M. persicus*.

**Habitat.** Frequents a variety of habitats in open and closed country near water: mangrove, tidal estuaries, margins of woodland, forest clearings, lakeshores, river valleys, plantations, farmland, paddyfields, suburban gardens.

**Food and Feeding.** Eats honeybees (*Apis*), wasps, hornets (including *Vespa orientalis*) and a variety of other hymenopterans, beetles, bugs, flies, moths, butterflies (including the noxious *Danaus chrysippus*), and numerous dragonflies (including the large *Crocothemis servillea*); occasionally takes small fish. Feeds by making long pursuit-flights from telephone wires, powerlines and tree-tops; makes height with fast, even wingbeats, glides, then twists abruptly after its prey; hornets are seized from below, with the bird's head thrown back and its bill pointing straight up. Returns to perch to beat prey against it and, if a stinger, rubs its tail on the perch to discharge venom. Flock often forages in continuous flight, usually high over trees.

**Breeding.** Breeds in Feb–Jun N of equator, Feb–May and Sept–Nov near equator; in New Guinea fledglings seen in May, but most breeding records in Sept–Nov. Colonial, with tens or hundreds of pairs together; sometimes in mixed colonies with *M. viridis* or *M. leschenaulti*; helpers not known, but social order would merit investigation. Excavates burrow in dry, sandy or loamy bank of waterway or in flat, grassy ground, roadside cutting, coastal dune, clay-pan, even in crumbling mud wall of building or in sea cliff; in New Guinea favours airstrips; burrow 1–2 m long, dug by both sexes. Clutch of 5–7 eggs; incubation and nestling periods uncertain.

**Movements.** A summer visitor to N Pakistan, N India and Himalayan States; common in Pakistan from Apr to Oct, flocks sometimes 1000-strong departing in mainly SE direction; although resident in Sri Lanka, better known there as a winter visitor from Oct or Nov to Mar or Apr. In SE Asia, too, it is a breeding visitor in N and a resident but also a conspicuous winter visitor in S; passage of over 150 birds an hour heading S occurs on W coastal plains of Malaysia in Aug–Oct, and large flocks return across Malacca Strait in Mar–Apr. Migrants have occurred on Andaman and Nicobar Is. Fairly common resident in Philippines, where also thought to be a winter visitor. Mainly resident in New Guinea, but thousands seen in R Bensbach region in Dec were probably immigrants.

**Status and Conservation.** Not globally threatened. Uncommon to locally common over forested regions in SE Asia, and common to locally abundant from Pakistan and Rajasthan to Bangladesh. Local and rather rare in New Guinea and New Britain. Present in numerous national parks throughout wide range, e.g. Kosi (Nepal), Kaziranga and Rajiv Gandhi (Nagarhole) (India), Yala (Sri Lanka), Khao Sam Roi Yot (Thailand), Kuala Selangor (Malaysia), Bali Barat (Bali), Lore Lindu (Sulawesi) and Wasur (New Guinea).

**Bibliography.** Abdulali (1950), Ali (1969, 1996), Ali & Abdulali (1945), Ali & Ripley (1983), Amstutz (1973), Avery & Penny (1978), Baker (1934a), Beehler *et al.* (1986), Bell (1986), Biswas (1961b), Coates (1985), Coates & Bishop (1997), Deignan (1945, 1955), Dharmakumarsinhji (1958), Dickinson *et al.* (1991), Duckworth *et al.* (1999), Étiénnecar & Hue (1978), Evans *et al.* (2000), Grimmett *et al.* (1998), Hoogerwerf (1964, 1970), Hoogerwerf & Siccama (1938), Inskipp, C. & Inskipp (1991), Inskipp, T. *et al.* (1996), Jayarajasingam & Pearson (1999), Kennedy *et al.* (2000), Kylänpää (2000), Lekagul & Round (1991), Lint & Stott (1948), MacKinnon & Philipps (1993, 2000), Madoc (1976), Marien (1950), van Marle & Voous (1988), Mason & LeFroy (1912), McClure (1998), Medway & Wells (1976), Mees (1982, 1986), Neelakantan (1948), Norris (1963), Phillips (1978, 1979), Raher (1977), Rand & Gilliard (1967), Ripley (1982), Roberts (1991), Robson (2000a), Round (1988), Silvius & Verheugt (1986), Smythies (1986, 1999), Sugathan & Varghese (1996), Tikader (1984), Ward (1968), Watling (1983), Wells (1999), Whistler (1949), White & Bruce (1986), Wildash (1968), Yang Lan *et al.* (1995), Zhao Zhengjie (1995).

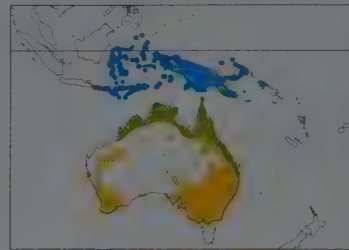
## 20. Rainbow Bee-eater

*Merops ornatus***French:** Guépier arc-en-ciel **German:** Regenbogenspint **Spanish:** Abejaruco Australiano  
**Other common names:** Rainbowbird, Australian Bee-eater**Taxonomy.** *Merops ornatus* Latham, 1801, New South Wales.

Taxonomically isolated, but thought to be distantly derivative of the superspecies that comprises *M. persicus*, *M. superciliosus* and *M. philippinus*. Monotypic.

**Distribution.** Breeds in Australia, including Rottnest I and SW islands in Torres Strait, and in E Papua New Guinea (at least Port Moresby area and Ramu Valley); possibly also in E Lesser Sundas. S populations winter in N of breeding range, mainly in and around New Guinea; also W throughout Wallacea.

**Descriptive notes.** 19–21 cm (with streamers, up to 7 cm more); 20–33 g. Distinctive: male mainly green, very glossy, with burnished crown and nape, rufous primaries with green outer edges and



per throat pale yellow, lower throat dull rufous-brown, merging into obscurely streaked light olivaceous breast.

**Habitat.** Sandy pasture, arable land, lightly wooded savanna, wooded environs of creeks and lakes, parks, gardens and green suburban areas. In non-breeding season, in New Guinea and New Britain, inhabits open suburbs, clearings in recently logged forest and airspace over forest canopy, seedling oil palm plantations, secondary growth at forest edge, giant bamboos by cattle paddocks, and waterways in undisturbed lowland rainforest.

**Food and Feeding.** Hymenoptera greatly preponderate in pellet samples; also eats beetles, bugs, flies, moths, butterflies, orthopterans, dragonflies and damselflies, all captured on the wing in forays from a leafy or leafless tree or telephone wire. Takes a few spiders, but whether from vegetation or airborne on silk is not known.

**Breeding.** Lays Sept in Papua New Guinea; in Aug–Nov and Jan–Mar in W Queensland, and mid–Nov to mid–Dec in S Australia. Breeds in loose colonies with nest-holes well separated, each pair in a territory defended against incursion by neighbouring pairs; in King's Park, Perth, 34 nests in 250 ha, some only a few metres apart. A good proportion of pairs have helpers; digging, incubation and feeding of young shared by both parents and any helper. Excavates burrow in level ground or the side of rut, ridge or low bank; burrow straight or curves a little to one side, in level ground with brood-chamber floor 40–42 cm below soil surface, and is 1–3.3 m long, average 149 cm, including terminal chamber 38 cm long, 20 cm wide and 8 cm high. Clutch of 3–7 eggs, usually 4–5, laid over 5-day period; incubation starts after second or third egg, and lasts for 21 days, sometimes more; most eggs hatch on same day; female takes minor share of all nest duties if pair has a helper, or major share if none.

**Movements.** Large numbers spend the austral winter in N Queensland and a few in SW Queensland, but main wintering grounds are in New Guinea. Emigrants moving N out of Australia concentrate at Torres Strait, where large flocks in Mar; huge numbers spread throughout open lowlands of New Guinea and its satellite islands, occurring at up to 2100 m. Passage N in New Guinea strong in Apr, birds travelling in flocks by day and on moonlit nights; cross mountain passes at 4000 m, and many continue farther W and N to Lesser Sundas, Moluccas and Sulawesi. A few winter in Solomon Is, and vagrants have occurred in Palau Is, Caroline Is and Ryukyu Is. Return migration in Sept–Oct, and sometimes great mortality in Torres Strait islands if birds encounter head winds.

**Status and Conservation.** Not globally threatened. Widespread in E New Guinea and Australia except in deserts and heavily forested regions, and is seasonally common and locally abundant in nearly all areas; common on New Hanover in 1999. Breeding-season densities of 12–33 birds/km<sup>2</sup> near Port Moresby and up to 32 birds/km<sup>2</sup> near Perth. Locally common in Sulawesi during austral winter. Present in several national parks, e.g. Wasur (New Guinea) and Royal, Wyperfeld, Kalbarri and Kakadu (Australia).

**Bibliography.** Beehler (1978), Beehler *et al.* (1986), Bell (1969, 1970e, 1975a, 1982c), Berggy (1978), Blakers *et al.* (1984), Calver *et al.* (1987), Carruthers (1975), Coates (1985), Coates & Bishop (1997), Conrie-Smith (1930), Courtney (1971a), Diamond (1972), Draffan *et al.* (1983), Filewood *et al.* (1978), Fraser, T. (1982), Garnett (1985), Gill (1970), Gilmore *et al.* (1979), Guthrie (1969), Higgins (1999), Inskipp *et al.* (1996), Isherwood *et al.* (1997), James (1968), Johnstone & Storr (1998), Johnstone *et al.* (1996), Klapste (1980), Kloot & Aston (1983), Koenig (1968), Lane (1963), Lea & Gray (1935), Lill (1993), Lill & Fell (1997), McKay (1969), Mees (1982), Morris (1976, 1977), Nicholls & Rook (1962), Peckover & Filewood (1976), Rand (1942b), Rand & Gilliard (1967), Rose (1997), Rozendaal & Dekker (1989), Saffer & Calver (1997), Schodde & Tidemann (1986), Serventy & Whittell (1976), Smith *et al.* (1978), Storr (1984a, 1984b), Tolhurst (1996), Waterman (1965), Waterman & Llewellyn (1968), Wheeler (1973), White & Bruce (1986).

## 21. Blue-throated Bee-eater

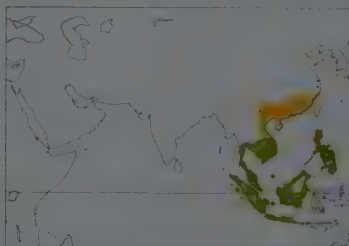
*Merops viridis***French:** Guépier à gorge bleue **German:** Malaienspint **Spanish:** Abejaruco Gorgiazul  
**Other common names:** Chestnut-headed Bee-eater**Taxonomy.** *Merops viridis* Linnaeus, 1758, Java.

Relationships uncertain. Javan population has sometimes been considered subspecifically distinct on plumage, with race *sumatranus* consequently resurrected to include all other populations herein placed in nominate; however, detected differences appear to be related merely to age or wear. Two subspecies currently recognized.

**Subspecies and Distribution.**

*M. v. viridis* Linnaeus, 1758 – SE China (including Hainan), S Thailand and Indochina (except much of Laos) S to Sumatra, Java, Borneo and N Natuna Is.

*M. v. americanus* P. L. S. Müller, 1776 – Philippines.



**Descriptive notes.** 21 cm (with streamers, up to 9 cm more); 34–41 g. Nominative race with crown and mantle dark mahogany, chin, throat and cheeks blue; back, wings and lower scapulars green, black band across trailing edge of wing; tertials and inner greater coverts fade to blue; wing long and pointed; lower back, rump and uppertail-coverts azure-blue, each feather white at base and grading to light blue distally; tail blue, streamers pale blue with white shaft subterminally and dusky blue terminally; iris red-brown. Sexes alike. Juvenile differs from adult in having forehead, crown, nape and mantle uniform dark green, chin

straw-coloured, cheek colour varying from straw to pale blue, underparts bluer; juvenile moult



protracted, some birds still have some green feathers on crown and nape 9 months after fledging. Race *americanus* has crown and mantle rich rufous, cheeks pale blue, chin and throat green.

**Habitat.** Beach-front scrub, dunes, pasture, farmland, suburban gardens, tin-tailings, sandy clearings and riversides in the lowlands; in winter, some birds occur in forest canopy and clearings at up to 670 m in altitude, and in saltwater channels in coastal mangrove forest.

**Food and Feeding.** Feeds on honeybees (*Apis*) and other hymenopterans, flies, beetles and bugs, some very large (up to 42 mm long); on Penang I, Malaysia, 90% of insects brought to nests were large dragonflies; quite often splash-dives into water, sometimes to bathe, but also thought to take small fish and insects; small bones, perhaps of a lizard, have been found in pellets. Watches for passing insects from perch in tall tree, or on telephone line or powerline, and makes dashing pursuit-flight, returning with prey to the perch in order to immobilize it by beating or, if a bee, to deventom it by rubbing; also hunts in continuous flight aloft, often in large flocks, hawking for small, swarming insects, which are evidently swallowed whole. Gathers at jungle fires to feed on fleeing insects, and at termite and ant hatches, sometimes hovering to pick insects from vegetation before they have taken flight. Flocks said to travel ahead of swift-moving tropical storms, probably to exploit insects carried up in turbulent air. Adults forage up to 24 km away from nesting colony.

**Breeding.** Eggs laid from Feb to about Apr in Borneo, in mid-Apr to mid-Jul in mainland Malaysia, and in Jan, May, Sept and Oct in Java. Usually nests in large colonies, of up to 1000 birds, nest-holes within 1 m of each other. Excavates in sandy soil in flat ground, coastal dune or shelving beach just above tideline, also in flat sandbank on river island or in dried-out watercourse; burrow generally 1-1.5 m long, but in Borneo some measured up to 2-7 m and 4-5 m, longer than recorded for any other bee-eater. Clutch of 3-6 eggs, usually 3-4, laid at intervals of 2-3 days, entire clutch hatching over 3-9 days; both parents incubate clutch and feed young; nestling period c. 30 days. Brood-members staggered in size, and youngest, smallest ones often starve to death; in small colony near Kuala Lumpur, average of less than 2 young fledged/nest.

**Movements.** Resident but dispersive, nomadic or locally migratory in Philippines, Java and Sumatra. Migratory farther N, being summer visitor to China and much of Indochina and partial migrant in S Thailand and Malay Peninsula; in the last region, a post-breeding exodus from coastal lowlands, and flocks migrate S by day in Aug-Oct and return N in Mar-Apr, when local birds are breeding.

**Status and Conservation.** Not globally threatened. Very little information regarding density and abundance of this species; it is widespread, with a huge latitudinal breeding range, and in many regions is regarded as common. Breeding success appears to be low in Malaysia, but no evidence that its numbers are declining or that its status is changing. Present in several national parks, e.g. Bach Ma (Vietnam), Taman Negara and Bako (Malaysia) and Way Kambas and Gunung Leuser (Sumatra); also in other protected areas, e.g. Khao Nor Chuchi (Thailand).

**Bibliography.** Avery & Penny (1978), Baker (1934b), Bangs & Penard (1923), Bryant (1983b), Bryant & Hails (1983), Bryant *et al.* (1984), Cansdale (1979), Delacour & Mayr (1946), Dickinson *et al.* (1991), Duckworth *et al.* (1999), Étiénope & Hie (1978), Hellebrekers & Hoogerwerf (1967), Inskipp *et al.* (1996), Jeyarajasingam & Pearson (1999), Kennedy *et al.* (2000), King *et al.* (1975), Lekagul & Round (1991), MacKinnon & Philipps (1993, 2000), Madoe (1976), van Marle & Voous (1988), McClure (1998), Medway & Wells (1976), Molesworth (1952), Parrott & Andrew (1996), Rabor (1977), Riley (1938), Robson (2000a), Round (1988), Smythies (1999), Stauder (1989a, 1989b, 1989c, 1994, 1996), Stepanyan (1995), Wells (1999), Yang Lan *et al.* (1995), Zhao Zhengjie (1995).

## 22. Bay-headed Bee-eater

### *Merops leschenaulti*

**French:** Guépier de Leschenault **German:** Braunkopfspint **Spanish:** Abejaruco Cabecirrufo  
**Other common names:** Chestnut-headed Bee-eater

**Taxonomy.** *Merops Leschenaulti* Vieillot, 1817, Java; error = Sri Lanka. Relationships unclear. Three subspecies recognized.

#### Subspecies and Distribution.

*M. l. leschenaulti* Vieillot, 1817 - S India and Sri Lanka; N India and Nepal E to SC China (Yunnan) and Indochina and Malay Peninsula.

*M. l. andamanensis* Marien, 1950 - Andaman Is and nearby islands of Great and Little Coco.

*M. l. quinticolor* Vieillot, 1817 - Java and Bali W into S Sumatra.



**Descriptive notes.** 20 cm; 23-33 g. A distinctive, smallish bee-eater with long wings but without long tail-streamers. Nominative race with bay-brown crown and mantle, green wings with broad black band over trailing edge, azure rump; black mask, yellow chin, cheeks and throat, rufous lower throat, thin black gorget; upper breast yellow, lower breast green, belly blue-green, bluer towards undertail-coverts; iris red. Sexes alike. Juvenile has forehead, crown and mantle green, not bay-brown, and nape and sides of crown rufous, tinged with green; gorget line dusky or rufous, not black. Race *andamanensis* larger, with mask reduced, and sides of

breast rufous; *quinticolor* has mask mostly chestnut, with lower throat yellow.

**Habitat.** Typically found in clearings and open spaces in forested country; also well-wooded open countryside, plantations, large gardens, beach scrub, and along riversides, roadsides, railways and mule paths.

**Food and Feeding.** Not well known; eats honeybees (*Apis*), wasps, ants, termites, dragonflies, butterflies and grasshoppers, all taken airborne. Forages by fly-catching from a bush-top, wire or bare branch; freely uses telephone wires and fences.

**Breeding.** Eggs laid in Feb-Jun. Loosely colonial, with c. 10-100 nests relatively close together, or single nests every few hundred metres along a roadside or bank. Both sexes dig nest-burrow in flat, open, sandy ground, shelving sandbank by river, or in vertical bank by river, drain or road cutting; in high cliffs, nests tend to be sited near top, 3-6 m above ground or water; burrow 45 cm long in hard earth, up to 3 m long in soft earth, in flat ground declines steeply then levels off to run c. 25 cm below surface, and in cliffs inclines gently for some 50 cm then becomes horizontal; digging may last for almost 1 month. Clutch of 4-8 eggs, 4-5 in Sri Lanka, usually 6 in N India; incubation by both sexes, period not known, with shifts of c. 10-25 minutes; nestling period not known.

**Movements.** In general resident, but marked migrations in some regions. In India, vacates monsoon-rainfall areas in Jun-Sept; some birds resident in Nepal, but most are visitors in Feb-Oct, breeding in spring. Mainly a spring-summer visitor in N Myanmar, and in Malay Peninsula local residents are augmented by winter visitors in Sept-Apr.

**Status and Conservation.** Not globally threatened. Common at least locally throughout huge range. Unusually high adult survival rate, of 80% on Penang I, Malaysia. As with most or all open-country

bee-eaters, it is likely that densities and abundances have increased with man-induced changes to the land over the centuries; species appears to be colonizing S Sumatra. Present in numerous national parks, e.g. Chitwan (Nepal), Corbett and Periyar (India), Yala (Sri Lanka), Khao Yai and Kaeng Krachan (Thailand), Nam Bai Cat Tien and Bach Ma (Vietnam) and Bali Barat (Bali). Race *andamanensis* reported to be common in Andamans in mid-1980's.

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## 23. European Bee-eater

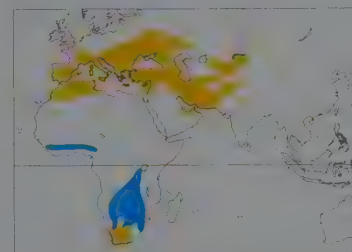
### *Merops apiaster*

**French:** Guépier d'Europe **German:** Bienenfresser **Spanish:** Abejaruco Europeo  
**Other common names:** Golden/Eurasian Bee-eater

**Taxonomy.** *Merops Apiaster* Linnaeus, 1758, southern Europe.

Relationships unclear. Monotypic.

**Distribution.** NW Africa (Morocco E to Libya) and SW Europe (Iberia) E to W Russia and C & SW Asia (E to L Balkhash and L Zaysan in Kazakhstan), S to Afghanistan and Oman; also S Namibia and South Africa. Winters at lower latitudes in tropical Africa.



**Descriptive notes.** 28 cm (with streamers, up to 2.5 cm more); 44-78 g. Highly distinctive with multicoloured plumage. Male has chestnut cap and mantle, yellow throat with black gorget, greenish-blue underparts; scapulars and rump flaxen; long uppertail-coverts the same green as tail, latter with streamers; primaries and their coverts and tertials green to green-blue, but rest of upperwing mahogany; dusky band along trailing edge of wing; iris red-crimson, mouth flesh-pink. In eclipse plumage in Aug-Oct, soon after breeding in Europe, crown, gorget and scapulars are green-tinged and mantle, back and rump green; non-breeding plumage

rather duller than breeding. Female tends to have scapulars and lower back greener, less flaxen, than male, lesser wing-coverts less intensely green, rufous median and greater coverts edged green, and yellow throat and turquoise breast and belly paler; tail-streamers up to 1.8 cm. Juvenile pale, with all of adult's chestnut and rufous parts suppressed by green except sometimes on crown, and "V" mark formed by scapulars, back and rump light green, not flaxen; iris brown.

**Habitat.** In Europe, broad river valleys, pasture and cultivated land with shelter-belts and scattered trees; sunny hillsides, meadows, clover fields, plains, dissected steppe, shrubby riverbanks in semi-desert, and practically any open and well-timbered country, such as cork-oak woods, olive groves, tamarisks, rice fields, cereal and root crops, and Mediterranean macchia scrub. Also savanna, lakeshores and farmland in Africa.

**Food and Feeding.** Diets have been studied repeatedly in great detail in many countries in Europe in relation to foraging energetics, in Asia in relation to apicultural economics, and in Africa to determine seasonal and regional variations. Relies largely on bumblebees (*Bombus*) and honeybees (*Apis*) in Europe, and on honeybees, wasps of many families and stingless bees in Africa, but takes most other orders of insects as opportune; in fact, probably eats all day-flying insects between c. 5 mm and 50 mm long, whether stinging, fast, high-flying, or otherwise; half of prey items are 10-15 mm long. Nestlings are fed larger insects than those consumed by adults, particularly if latter are foraging more than a few hundred metres from nest. An adult catches a considerable diversity of insects on an average day, but, where a single species is abundant, will prey on that for long time; e.g. bumblebees over clover fields, honeybees at apiaries, dragonflies over swamps, cicadas in *Acacia* woods, or a hatch of termites or swarm of locusts. Attracted to fires to exploit fleeing insects, and sometimes follows a person or vehicle to hunt insects put to flight. Forages from vantage point on tree, telephone wire or fence, making lengthy forays after a passing insect, seizing it after short dashing chase, and bringing it back to the perch to beat its head and, if a stinging bee or wasp, rub its tail to deventom it. Also frequently hunts for small insects in continuous flight aloft.

**Breeding.** Lays in May-Jun in Europe, from Apr in NW Africa, in Jun-Jul in Uzbekistan, and in Oct-Nov in South Africa. Pair-members usually stay together for life. Sometimes solitary but often in loose aggregations or well-defined small or large colonies, in Asia often mixed with cliff-breeding colony of *M. persicus*; c. 1 in 5 pairs has a helper, which is usually an adult son. First-year birds pair up on African wintering grounds and migrate together. Soon after arrival in spring at male's natal site, the pair with any helper excavates 1 or 2 false starts then the definitive nest-burrow, occasionally in flat or sloping sandy ground but generally in earthen cliff; 7 kg, sometimes 12 kg, of earth is kicked out of entrance as digging proceeds, and whole process takes 10-20 days; burrow oval in section, 7 cm high, 9 cm wide, straight or gently curving to one side, horizontal or, in cliff, slightly inclining, and 70-150 cm long. Clutch of 4-10 eggs, average 5 in France, 6 in Hungary, 5-8 in Russia, 6 in South Africa, laid at intervals of 1-2 days; incubation begins sporadically with first egg, persistently with third, period 20 days or more in Palearctic, yet sometimes as short as 13 days in South Africa; both sexes have a brood patch and incubate by day; in Palearctic, at night only female is in nest, whereas in South Africa both parents present; incubating bird checks eggs in complete dark by passing bill tip across them; incubation shifts 10-60 minutes in Palearctic, but 2-3 hours in South Africa; hatching takes 2-6 days; chicks at first naked, pink and blind, later covered in spiky grey feather sheaths, then juvenile feathers, by which time nestlings can see and are mobile and aggressive; fed by both parents and any helper, achieving adult weight of c. 55 g in 15-17 days, at 20-25 days weighing 60-70 g, and thereafter becoming lighter as feeding diminishes and plumage growth continues; young leave nest on day 30 or 31, at 2-3 g above mean adult weight. European birds commonly rear 4 chicks, but South African ones average only 1.

**Movements.** All populations migratory. Spanish and French birds fly via Strait of Gibraltar down Moroccan Atlantic coast into W Africa, and Italian and Sicilian birds probably cross to Tunisia and, with NW African populations, head for W African wintering grounds; ringing returns show that Balkan and Caspian birds pass through Cyprus and the Levant and head up R Nile and through Uganda to SE African wintering grounds; birds from Ryazan, Russia, pass through Georgia and



Cyprus; Asiatic populations either follow the Nile route or cross Arabia and Red Sea on a broad front. Family parties are thought to remain together on autumn migration. Flocks fly mainly by day, usually high up, often with *M. persicus*, and congregate at oases, on islands and along leading topographic features. In Cairo, Egypt, particular clumps of trees are used for roosting night after night by different flocks of migrants in succession, in both autumn and spring, 90% of migrants cross from Gibraltar to Morocco in 18-25 days, in Aug-Sept, with peak passage in second week Sept. Numerous on passage in E Africa in Sept-Nov and in Zambia in Oct-Nov; birds arrive in SW Cape in Sept-Oct and depart in Feb. South African birds are breeding at that time, and emigrate N to spend austral winter in Angolan and Zairean savanna at same time as European populations are returning through E Africa to Europe. In Ryazan, Russia, over 80% of birds return in spring to site of previous year's colony. Species recently recorded in Madagascar, late Nov 1996.

**Status and Conservation.** Not globally threatened. Locally common and widespread over much of its range. On basis of density estimates in Hungary and counts of autumn migrants at Gibraltar, and allowing for a third or a fifth of breeding pairs having a helper, world population was estimated in 1980's at 4,000,000 birds pre-breeding and 13,000,000 post-breeding. More recent estimates based on improved knowledge of Iberian and Balkan densities, but not allowing for helpers, give pre-breeding population of the order of 240,000-1,100,000 birds. S African breeding population is thought to number 20,000 birds, and even globally insignificant population in Oman may be as many as 4000, so world population may richly exceed 1,100,000, particularly as it now seems that populations E of the Caspian may have been underestimated. Absolute numbers aside, what matters for conservation policy is how regional densities are faring; European countries appear to show contradictory trends, but reliable quantitative data are still lacking nearly everywhere. Large numbers are known to be killed as pests, for eating and for sport, but greater threats in the long term likely to be depression of insect faunas by broadcast application of pesticides on both breeding and wintering grounds, increases in large-scale crop monoculture, the canalization of rivers with loss of riverbank nesting sites, and the development of wilderness land. Population of South Africa appears to be plummeting, with several colonies disappearing and others diminishing very rapidly.

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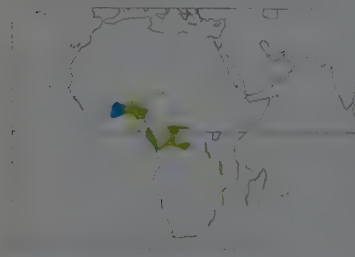
## 24. Rosy Bee-eater

### *Merops malimbicus*

**French:** Guépier gris-rose **German:** Rosenspint **Spanish:** Abejaruco de Malimba

**Taxonomy.** *Merops malimbicus* Shaw, 1806, Malimbe, Cabinda, Angola. Monotypic.

**Distribution.** Nigeria S to Equatorial Guinea, Gabon, Congo and Cabinda (N Angola), and W & WC Zaire. Regular migrant W to W Ghana.



derparts dull dirty pink, buffy on belly.

**Habitat.** Inhabits airspace above rainforest and mesic savanna woodland, foraging around trees emergent from the canopy, in clearings and over broad rivers and adjacent wooded country, also over dams, reservoirs and farmland; in between forays tends to perch high in trees. Breeds on large rivers, where perches lower in vegetation and commonly sits on ground.

**Food and Feeding.** Small flying ants greatly predominate in diet; however, species also consumes large numbers of honeybees (*Apis*), and vespid, spider-hunting and sand wasps, butterflies, dragonflies, damselflies, termites, grasshoppers, crickets, water beetles, flies, and bugs. The most aerial of

**Descriptive notes.** 25 cm (with streamers, up to 5 cm more). A long-winged bee-eater, with unmistakable plumage coloration. Adult slate-grey above; vivid pink below; black mask with white cheekstripe; tail dull carmine, but exposed parts soon bleach to same grey as rest of upperparts; iris carmine-red. Sexes alike, but female streamers c. 3.5 cm long. Juvenile grey above, wing-coverts, tertials, back and rump feathers very narrowly pale-fringed and with slight blue-green tinge; tail dark grey-brown with dull carmine wash along feather shafts; mask dark grey rather than black; cheekstripe buffy, not pure white, and poorly defined; un-

all bee-eaters. Insects caught mainly in continuous wheeling flight, but also as a result of fast forays for some distance starting from an elevated perch, usually a treetop; some insects appear to be eaten aloft, and larger ones are carried back to a perch to be immobilized and devoured.

**Breeding.** Lays in May-Jun on R Niger and probably in Feb-Apr on lower R Congo; on coast of Cabinda (N Angola) breeds soon after arrival in May; in coastal Congo, digging in Oct. Nests in huge colonies in shelving sandbars exposed by falling waters of broad rivers, and has nested in coastal bluffs: few colonies found, one contained c. 18,500 nest-holes, another c. 23,700, two c. 15,000 holes each, and one found in 1933 may have well over 25,000 holes: one colony measured 330 x 33 m; on bare sand nest-holes evenly scattered, at c. 195-240 holes/100 m<sup>2</sup> or c. 2/m<sup>2</sup>; nests are aligned, the entrances mostly facing same quarter. Burrow 180-195 cm long, declining at 16° to depth of 25 cm, then levelling off and ending in oval egg-chamber with floor c. 50 cm below sand surface. Clutch of 2 eggs. No further details known. In some areas old colonies apparently taken over by African River Martins (*Pseudochelidon eurystomina*).

**Movements.** Present at breeding sites on R Niger and R Benue in Nigeria in Apr-Jun or May-Jul, and after breeding disperses rapidly, some birds moving to 10° N but most moving S to the forest zone, where occurs from late Jun to early Apr, being common in Sept-Mar. In forest zone in Nigeria a well-known migrant of predictable occurrence, but in savanna between rainforest and the great rivers it appears only erratically. Resident in some forested areas. A non-breeding migrant to forest clearings and coastal savanna in Ghana in Oct-Mar, occasionally in Jul-Sept. Resident on upper R Congo; at Malimba, on coast 80 km N of R Congo mouth, a breeding visitor in May-Aug; on Fernand Vaz coast of Gabon, it is in evidence mainly in Sept-Nov. Vagrant in Ivory Coast.

**Status and Conservation.** Not globally threatened. May merit reclassification as threatened species. Locally common in parts of Ghana, Nigeria, Gabon, Congo and Zaire, but absent or sporadic in other parts: not known to breed W of Nigeria; uncommon in Togo and Benin, unknown in Cameroon, poorly known elsewhere. Considering that this is one of Africa's most spectacular birds, it remains remarkably under-studied and under-valued. River sandbars where it nests are submerged by rising water after each breeding season, so nests have to be dug anew every year; in one case, same sandbar was used for at least 4 years. Most sites are probably traditional; known sites need to be monitored, and further breeding colonies must await discovery. Species' status could be better defined with surveys of R Niger and E Benue in Nigeria, and the Congo, Kasai and lower Oubangui rivers in Zaire and Congo. Colony of 1000-1500 birds located in Konkouati Reserve, Congo, in Oct 1996.

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## 25. Carmine Bee-eater

### *Merops nubicus*

**French:** Guépier écarlate **German:** Karminspint **Spanish:** Abejaruco Carmesí

**Other common names:** Northern Carmine/Nubian Bee-eater (*nubicus*); Southern Carmine/Ruby Bee-eater (*nubicoides*)

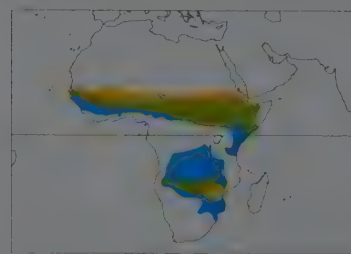
**Taxonomy.** *Merops nubicus* J. F. Gmelin, 1788, Nubia.

Races commonly raised to the rank of separate species, but identical in voice, ecology, and breeding and migratory habits, and morphological and plumage differences considered relatively insignificant. Two subspecies recognized.

**Subspecies and Distribution.**

*M. n. nubicus* J. F. Gmelin, 1788 - Senegal E to Eritrea, and S to N Kenya; in austral winter farther S in N tropics and in E Tanzania.

*M. n. nubicoides* Des Murs & Pucheran, 1846 - S Angola, extreme NE Namibia (Caprivi Strip) and S Zambia, E to S Malawi and C Mozambique; spends austral winter N to Burundi and S to N Natal.



**Descriptive notes.** 24-27 cm (with streamers, up to 9.5 cm more in nominate, 12 cm more in race *nubicoides*); 44-61 g. Distinctive, long-winged bee-eater. Adult nominate race has crown, chin, cheeks, rump and uppertail-coverts beryl-green, and throat dark olive-green, against light appearing respectively azure-blue and blackish or greenish-blue; black mask; exposed parts of tertials dull green-blue; otherwise rest of upperparts carmine-pink, wing with black trailing edge, 4-5 longest primaries with subterminal blue spot on outer webs; central tail feathers longer than rest of tail, streamers not steeply attenuated and are 4 mm

wide at tip; belly carmine, becoming pale azure-blue on undertail-coverts; underwing-coverts cinnamon-buff; bill stout, black; iris red. Sexes alike, but female's streamers shorter. Juvenile has forehead and crown mid-blue, nape and upper mantle brown, lower mantle rufous, scapulars and tertials olive-brown with bluish edges, rump and uppertail-coverts greyish-azure, tail dull carmine, browner distally, with bluish fringes; mask black; chin and throat mid-blue, breast feathers brown with pale pink tips, belly and undertail-coverts very pale. Race *nubicoides* somewhat larger and 10-15% heavier than nominate, differs also in carmine-pink throat colour, longer streamers, and dark brown to black iris; juvenile with chin and throat pale pink or, rarely, pale blue.

**Habitat.** Bushy and wooded savanna, rivers, floodplains with oxbows and stands of trees, pasture and tiled fields with scattered timber, swamps, marshes, lakes and shores, mangroves, thornveld, and grassy plains carrying ungulates. Requires large expanse of riverside cliffs for nesting.

**Food and Feeding.** Eats a great variety of insects, often grasshoppers and locusts; takes numerous honeybees (*Apis*) and other hymenopterans; feeds its young on rather large insects, including shield-bugs, water-bugs, grasshoppers, wasps, carpenter-bees (*Xylocopa*), dung beetles, butterflies and cicadas. Forages mainly aloft, in effortless sailing flight, straight or in wide circles, only occasionally flapping; often soars falcon-like and rises on thermals; feeds at height of 50-100 m, in bouts of 5-10 minutes alternating with long rests perching on a tree. From a perch, gives chase to passing insect, either returning with it to the perch to beat it or continuing up to foraging altitude for a lengthy foray; uses large variety of quadrupedal mammals and a few large birds as animate perches, dashing aside to seize any insect put to flight from the grass. Attracted to bush fires from afar, flying boldly in and out of billowing smoke in pursuit of fleeing insects. Often splashes down on to water, generally to bathe, but known also to catch small fish near surface, and has even been seen diving right under the water in the style of a kingfisher. Travels far afield in search of food, staying with a hatch of suitable insects to exploit it fully.



**Breeding.** Lays at start of rainy season at low latitudes, some weeks before it at highest latitudes: in Nigeria, in Apr in S of range and May-Jun in N; in S Africa mainly in Sept-Oct; in some places burrows are dug 4-5 months in advance of egg-laying. Breeds in large, dense colonies, usually of hundreds of nests, sometimes thousands, in cliff by meandering river, favouring tall, fresh-cut sand cliffs free of vegetation, but sometimes in level ground; up to 60 nest-holes/m<sup>2</sup> of cliff face and 6/m<sup>2</sup> in flat ground; exactly the same cliff site can be used for decades, other sites shift a few hundred metres from year to year. Both sexes excavate; burrow straight, slightly declining, 6 cm in diameter, 1-2 m long but once 3-7 m, the oval chamber at end unlined, not angled but aligned with burrow. Clutch of 2-5 eggs; when 2 eggs, second laid 48 hours after first; in 3-egg clutches intervals are of c. 43 and 53 hours; incubation period unknown; nestling period probably c. 30 days.

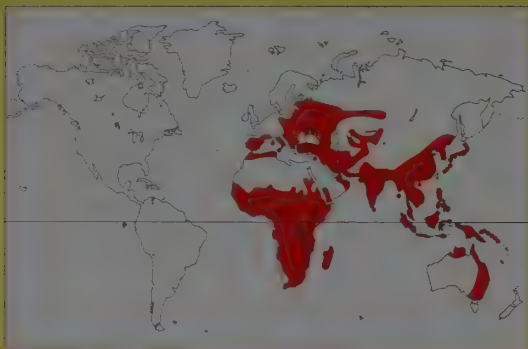
**Movements.** In S tropics a three-stage migration: arrives on breeding grounds in Aug-Sept, and after breeding disperses S into N and E Botswana and Transvaal from Dec onwards; reporting rate in NE Namibia, Botswana and Zimbabwe low in May-Jul, high in Aug-Nov, highest in Dec-Jan, then falls in Feb-Apr; in Transvaal scarce in Apr-Sept, common in Oct-Mar, commonest in Jan-Feb; most birds quit the region in Mar and migrate N to spend austral winter, Mar-Aug, in Zambia, Malawi, much of Angola, SE Zaire and Burundi. Migrations in N tropics and E Africa also three-staged, but with breeding and movements displaced by 6 months; in parts of range, and possibly throughout, after breeding the species disperses widely, moving up to 200-250 km, generally towards N.

**Status and Conservation.** Not globally threatened. Locally common along larger rivers throughout breeding range. Nesting colonies are an ornithological and tourist attraction; many are in traditional sites, and at least 140 colonies were known in early 1980's. That is possibly no more than 10% of all that exist; 34 colonies with some 11,300 birds were found on 208 km of the R Zambezi in 1991. If pressured, colonies can be abandoned; in Zimbabwe, one at Beatrice, famous for 40 years, was abandoned in 1966 after a variety of human disturbances, and another, at Chipandaure, was deserted in 1991 following 3 years when 1000 birds were ringed. Other colonies outside national parks in Zimbabwe have been exploited for food, to the point of extinction. Many colonies on

R Zambezi were adversely affected by rising lakes behind Kariba and Cabora Bassa (Mapata) Dams; those in Mana Pools National Park suffer greatly from bank collapse caused by wind- and speed-boat-generated wave action, exacerbated by constant changes in water level driven by hydro-electricity demands; bee-eaters are also vulnerable to insect scarcity after poor rainy seasons. Present in numerous national parks in both N and S of range, e.g. Niokola Koba (Senegal), Comoe (Ivory Coast), W (Niger), Waza (Cameroon), Dinder (Sudan) and Awash (Ethiopia), and South Luangwa (Zambia), Liwonde (Malawi), Hwange and Mana Pools (Zimbabwe), Chobe (Botswana) and Kruger (South Africa).

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Class AVES  
Order CORACIIFORMES  
Suborder CORACII  
**Family CORACIIDAE (ROLLERS)**



- Medium-sized, brightly coloured birds with short, hook-tipped bill, short legs, medium-length wings, and sometimes long tail-streamers.
- 25-40 cm.



- Old World.
- Open woodland, savanna woodland, forest edge, some species in lowland rainforest or at its margins; in warm climates.
- 2 genera, 12 species, 31 taxa.
- 1 species threatened; none extinct since 1600.

### Systematics

The Coraciidae are highly conspicuous birds, but, in spite of the fact that throughout most of Africa and in parts of Asia and Australia they are not uncommon, the family remains poorly studied. This is true not only with regard to observations in the field, but also in respect of research on the various species in the aviary and the laboratory. One consequence is that the evolutionary history of the family, its origins and relationships, as well as the inter-relationships of the dozen species, remain matters of some conjecture.

A suite of anatomical characters shows that the typical rollers, the family Coraciidae, are related to two other small families that carry the name roller, namely the cuckoo-rollers (Leptosomidae), represented by a single species (*Leptosomus discolor*), and the ground-rollers (Brachypteraciidae). There is little doubt that the Coraciidae are also related, if more distantly, to the kingfishers (Alcedinidae), the motmots (Momotidae), the todies (Todidae) and the bee-eaters (Meropidae). They are all hole-nesting perching birds; but so, too, are the trogons (Trogonidae), the Hoopoe (Upupidae), the woodhoopoes (Phoeniculidae), the hornbills (Bucerotidae), the jacamars (Galbulidae), the toucans (Ramphastidae), the barbets (Capitonidae), the honeyguides (Indicatoridae) and the woodpeckers (Picidae), which share several of the rollers' features. Therein lies the problem. The many families, some Neotropical and others Palearctic, some of them with highly specialized feeding and breeding habits, have generally been divided between two great orders, the Coraciiformes and the Piciformes. It now seems, however, that many of their shared characters result from evolutionary convergence, with parallel adaptations to tree-living and to tree-hole and ground-hole nesting, and currently the coraciiform/piciform families are generally placed in as many as six separate orders. Their common origin should probably be sought well before Eocene times.

To many ornithologists, rollers epitomize ideas about early, primitive perching birds. If that great order of perching birds, the Passeriformes, often referred to as the songbirds, did not evolve from ancient rollers or roller-like birds, it is nevertheless an attractive notion that it may well have done so. In many regards, rollers would appear to be rather simply organized, generalized, and "primitive". Most are stolid, sit-and-wait predators of small vertebrates and large arthropods, particularly insects taken from the surface of the ground more or less below the perch.

Their voices are raucous, and their vocalizations lack the diversity and structure associated with those of the songbirds. Their nests are simple pads of vegetable material cast on to the floor of a hole, and their breeding organization is by no means sophisticated. In a world of specialists, it is hard to see how rollers have held their own, but that is what they have done, for by the criteria of diversity and individual abundance they must be rated a successful family.

The twelve coraciid species live in the Old World tropics. They are mainly Afrotropical, with a few Asiatic, and one pene-



The twelve extant species that comprise the roller family are restricted to the Old World, particularly its tropical regions, and are shared between two well-defined genera. One of these, *Eurystomus*, to which this juvenile Dollarbird belongs, is characterized by a broad bill, which is brightly coloured in adults. Other adaptations include long wings that furnish them for aerial foraging, and short legs. The genus contains only four species, one pair Asian and Australasian and another pair African, each including one widespread taxon and a closely related but geographically restricted forest specialist.

[*Eurystomus orientalis pacificus*, Brisbane, Queensland, Australia.  
Photo: Brian J. Coates]



The Indian Roller belongs to the genus *Coracias*, which numbers eight species; these somewhat resemble the entirely unrelated crows (*Corvus*), but for their gorgeous plumage. In general, they are variations on a theme of greenish and rufous, purple, dark blue and azure. The bills of *Coracias* species are slightly longer and much less broad than those of *Eurystomus* species and are blackish in adults, while the legs are slightly longer and the wings shorter. These morphological differences relate to the infrequency with which they forage aerially, tending instead to snatch prey from the ground. Several features, including large heads on short necks and short legs terminating in weak feet, are common to both these genera and thus characterize rollers in general.

[*Coracias benghalensis indicus*, India.

Photo: Art Wolfe]



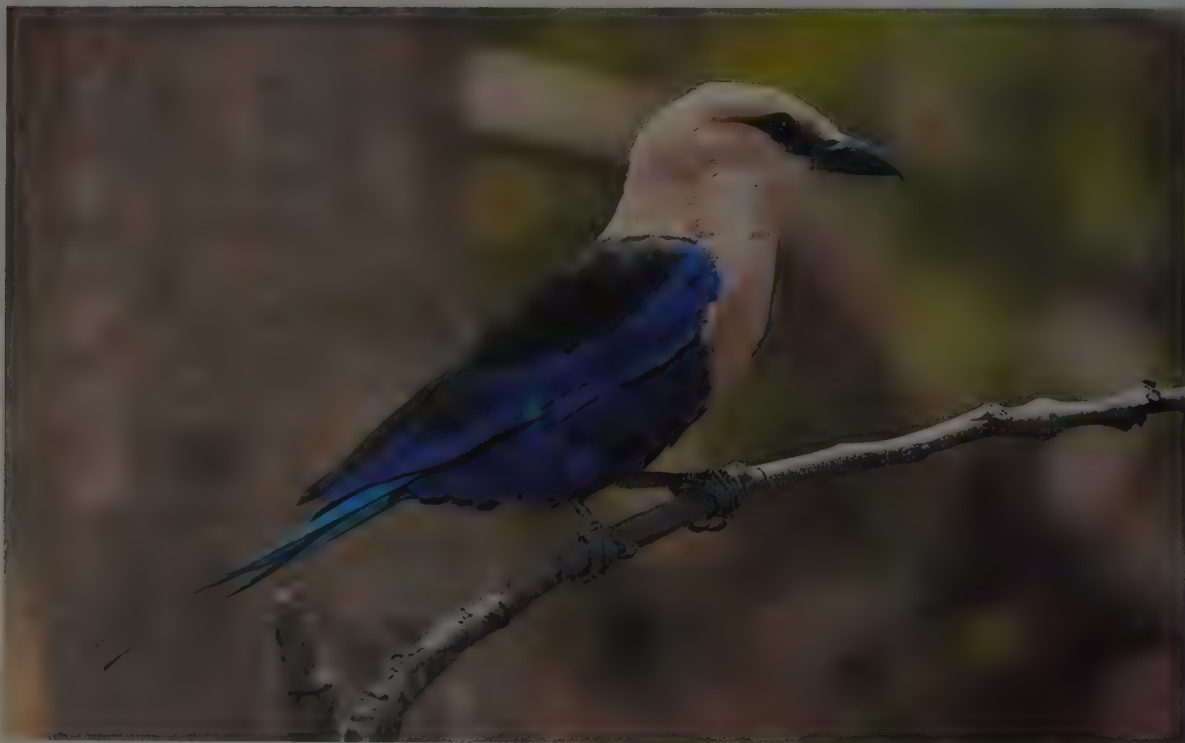
trating Australia nearly to Tasmania. Their relatives the Cuckoo-roller and the ground-rollers are also Afrotropical, and live close to Africa in the Malagasy subregion. Eight rollers, the sitters and waiters mentioned above, make up the genus *Coracias*; the four "broad-billed" rollers, combined in the genus *Eurystomus*, are sit-and-wait predators that are, additionally, far more lively and energetic aerial foragers. The Palearctic and essentially Afrotropical distribution of the various roller-like families suggests that they originated in ancient Africa. The few fossils that can confidently be ascribed to the family Coraciidae are, however, all European, as A. Feduccia has shown in a recent review. They are *Geranopterus alatus*, close to *Coracias*, from the late Eocene and Oligocene of France, and three unnamed coraciid rollers from the Middle Eocene of Germany. Some even older roller-like fossils are known from England and, surprisingly, from Wyoming in the United States; these are not coraciid rollers, but may be ground-rollers. *Prefica nivea*, a beautifully preserved fossil from the Lower Eocene of Wyoming, was at first thought to be very close to *Eurystomus*, but is now considered to be an oilbird (*Caprimulgiformes*).

*Coracias* and *Eurystomus* are both good, clearly defined genera. Each is uniform, but the two differ sharply, and there are no intermediate forms. They are similar morphologically except for bill shape, and they share the same basic colours of rufous, glossy dark blue and iridescent pale azure-blue, but they differ in their flight and foraging characteristics.

The European Roller (*Coracias garrulus*) of the western Palearctic looks and behaves very much like the Abyssinian Roller (*Coracias abyssinicus*) of the northern tropics of Africa, but it is larger, longer-necked, and without tail-streamers. It spends the non-breeding season exclusively in Africa, and it is probably a fairly recent derivative of ancestral *C. abyssinicus*

there. Four other species of *Coracias* are African, too, and the Abyssinian Roller is thought to be even more closely allied to one of them, the Lilac-breasted Roller (*Coracias caudatus*), than it is to the European Roller. While the breeding ranges of the European and Abyssinian Rollers are well separated by the Sahara, those of the Abyssinian and Lilac-breasted Rollers are suggestively parapatric, or are nearly so, since they apparently overlap in a belt 200 km wide across the Rift Valley in Ethiopia. It remains to be determined whether the last two species breed side by side in that belt or whether one of them is only a non-breeding visitor there; a hybrid between the two has been reported once from Ethiopia. These three rollers would seem to be of immediate common descent and so may be regarded as forming a superspecies, even though they do not comply with the other criterion of a superspecies, namely that its constituent taxa would be regarded by some modern systematists merely as subspecies.

The Lilac-breasted Roller is a widespread coraciid, with one subspecies, *lorti*, in Somalia having a lilac throat, and another throughout much of Africa south of the equator which has the throat and breast lilac-coloured. The latter embraces the range of the south-east African Racquet-tailed Roller (*Coracias spatulatus*), which has the throat and breast almost lilac in the east of its range but blue with lilac sides in the west, with a broad zone of intergradation in between. Some juveniles of these two roller species are very alike, having a buffish-lilac "plastron", or breast, streaked with white. A leading authority, P. A. Clancey, has shown that in all probability this type of plastron is a primitive character in the genus. Even adult Lilac-breasted and Racquet-tailed Rollers look rather alike. They often live in sight and sound of one another, although they prefer different types of woodland; it could be that the two species are



Perhaps the most divergent *Coracias* species is the striking Blue-bellied Roller of West Africa. Like other rollers, however, its legs are short and its feet relatively small, presumably because they function largely in perching, never being employed for hopping along a branch and only infrequently for shuffling on the ground. The head is the business end of rollers and, as befits their predatory nature, their bills are invariably robust and distinctly hook-tipped. Appended to the tail of the Blue-bellied Roller are two elongated streamers, a feature found in three other *Coracias* species but absent from *Eurystomus*.

[*Coracias cyanogaster*, Abuko Reserve, Gambia. Photo: K. A. Linnard/Aquila]

mutually less closely allied than each is to some other roller, perhaps the Abyssinian.

The Racquet-tailed Roller has a form, *weigalli*, which closely resembles the adult Lilac-breasted Roller of the nominate race, and is even more similar to its immature. The taxonomic status of *weigalli* remains to be finally resolved. Clancey has argued that it is a valid subspecies, but C. W. Benson and F. M. Benson, and later M. P. S. Irwin, concluded that specimens

of *weigalli* are merely half-moulted immatures of the species. C. H. Fry reviewed the Bensons' material, and the many skins in the Natural History Museum in Britain, and concluded that *weigalli* is geographically distinct from nominate *spatulatus*. There seems to be a 200-km-wide zone of hybridization between the two subspecies, from near Dar-es-Salaam, in east Tanzania, through south-west Tanzania and Malawi into central Mozambique; occurrences of *weigalli* in Zimbabwe may involve non-breeding migrants.

Two more *Coracias* species, the Blue-bellied Roller (*Coracias cyanogaster*) of West African *Isobertia* woodland, and the large Purple Roller (*Coracias naevius*), widespread in African wooded savanna, are independent species without obvious allies in the genus. In Asia, the western subspecies of the Indian Roller (*Coracias benghalensis*) looks a little like the Lilac-breasted Roller. Its eastern race, *affinis*, has been treated as a separate species, although in east Nepal it intergrades with nominate *benghalensis*. Interestingly, the purple and dark olive plumage of *affinis* adumbrates that of the final *Coracias* species, the Purple-winged Roller (*Coracias temminckii*), endemic to Sulawesi. While the latter is quite distantly removed from the mainland range of *C. benghalensis* *affinis*, and although there are conspicuous differences between the two in wing and tail patterns, it is very probable that *C. temminckii* is derivative of *C. b. affinis*.

With only four species, the broad-billed rollers of the genus *Eurystomus* can be dealt with rather summarily. The two Afrotropical ones, the Blue-throated Roller (*Eurystomus gularis*) and the Cinnamon Roller (*Eurystomus glaucurus*), are very alike, and have been regarded as representing a superspecies. One is a resident of the equatorial rainforest, and the other is a savanna-woodland migrant which sometimes breeds well within the range of the forest species. There are thus grounds for treating the two as independent species. Separated from them by the Indian Ocean is the Dollarbird (*Eurystomus orientalis*), with a vast breeding range in some ten subspecies, from south-west India to the Solomon Islands and from Manchuria to south-east Australia. In the North Moluccas, between Sulawesi and New Guinea, the resident coraciid, the Azure Roller (*Eurystomus azureus*), is sufficiently distinct to be seen as a separate species, although united with the Dollarbird in a superspecies. Where the genus originated, whether in Africa, Madagascar, Asia or Australasia, is a matter of guesswork.

The *Coracias* rollers are sometimes referred to as "true" rollers, on the grounds that members of this genus alone perform the spectacular display known as "rolling". They have rather a compact silhouette, with moderately broad wings and a fairly long tail, which in some cases sports streamers. They are good, strong fliers and demonstrate a fair degree of agility, although their flying skills are clearly overshadowed by the members of the longer-winged, more aerial genus *Eurystomus*. The Purple-winged Roller of Sulawesi, true to the habits of its genus, appears to carry out little aerial foraging.

[*Coracias temminckii*, Tangkoko-Dua Saudara, north Sulawesi. Photo: Brian J. Coates/Lynx]





The function of tail-streamers in *Coracias* rollers is unclear.

They are not likely to be aerodynamically influential, but they may assist balance while perching.

Perhaps more likely, however, is that elongated outer rectrices are sexually selected ornaments, or developed as badges of specific identity.

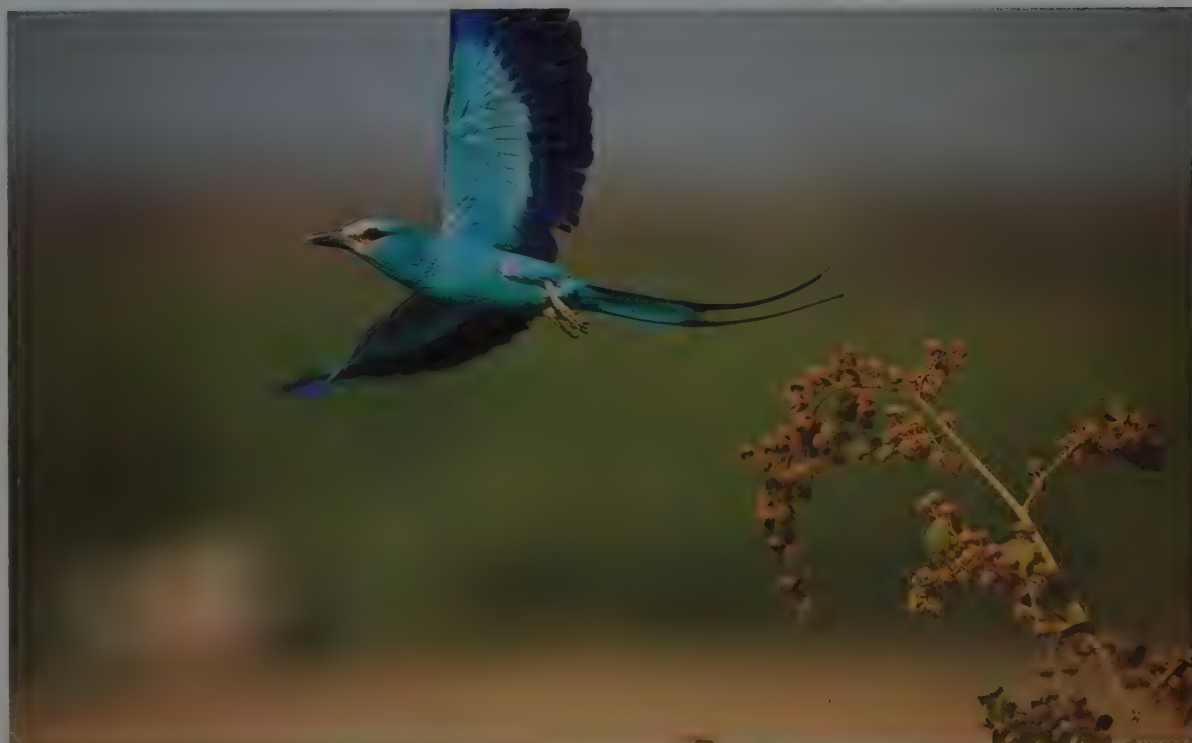
Long-range recognition of and by conspecific rivals and prospective mates is presumably helpful to individual rollers; and also, indirectly, to ornithologists!

In support of this idea, sympatric roller species tend to have different streamer design.

For example, this Abyssinian Roller has very long streamers while those of the Blue-bellied Roller (*Coracias cyanogaster*) are considerably shorter.

[*Coracias abyssinicus*, East Africa.

Photo: Xavier Eichaker/Bios]



### Morphological Aspects

Like other coraciiform birds, rollers are large-headed, short-necked, short-legged and weak-footed. They are essentially tree-perching birds and, although they barely walk or hop when on the ground to seize their prey, it does seem surprising that they do not have stronger legs or the powerful grip of the crows (*Corvus*), for example. When handled, a wild-caught roller may struggle quite strongly for a moment, but it then lies resignedly, and to the handler it does not give the impression of being a powerful sort of bird, while its toes have rather a feeble grip upon the finger. The leg is somewhat fleshy, the four toes being short, with curved, short, but moderately strong claws. Of the three forward-pointing toes, the inner and middle ones are tightly bound to each other by skin for about half of their length. The large head, short neck and robust bill must reflect sufficient concentration of power at the operative end of the bird for it to deal effectively with the hard and sometimes dangerous food items that it takes.

In general morphology, *Coracias* rollers stand comparison with the smaller crows, and in several languages the European Roller does indeed bear the vernacular name of "blue crow". The bill is much the same shape as that of a Eurasian Jackdaw (*Corvus monedula*), but, as befits a predator, it is more hook-tipped. By contrast, the broad-billed rollers of the genus *Eurystomus* possess a bill that is stouter, shorter, deeper and broader at the nostrils, and much broader at the corner of the mouth; it recalls the bill of some other species which prey on large insects, such as the broadbills (*Eurylaimidae*), the frogmouths (*Podargidae*) and even some swallows, namely those of the genus *Pseudochelidon*. The *Coracias* species have a black bill, while that of the broad-billed rollers is scarlet or bright yellow. Whether this colour difference is adaptive is not known, but the difference in shape can readily be related with the foraging techniques of the two genera. The *Coracias* rollers are sit-and-wait predators that fly down to the ground to seize their prey there. The *Eurystomus* species, on the other hand, pursue an insect through the air and generally crush and swallow it while they are still in flight, the greater width of their gape presumably making it easier to scoop the item out of the air. Since the prey of all coraciids often consists of large, strong, struggling beetles, which *Coracias* rollers immobilize by beating against hard ground or a branch, the broad-billed rollers, without the aid of a perch, need a deep bill for strength and a short one to concentrate the power of the bite.

Rollers do not hop along the perch, and seldom, if ever, swing about to face the other way. Apart from perching, they use their short legs for little more than occasional brief, shuffling leaps on bare ground in pursuit of a runaway prey. In the air, however, they are far more accomplished. The broad-billed rollers have a buoyant, undulating flight with deep flapping wingbeats and level glides. When chasing insects they are more falcon-like, closing the wingtip to make it pointed in fast downward glides and open-



The Racquet-tailed Roller shows the most highly developed streamers within the family. In this species, the streamers are up to 8 cm longer than the rest of the tail and they end in a bulbous, spatulate tip, which has a concave undersurface.

The juvenile bird lacks the streamers, and is generally a duller version of the adult, with a pinkish wash on the face, throat and breast, bespattered with white streaking.

Much the same pattern of coloration is evident on the race *weigalli*, and it has been suggested that this form may constitute merely some subadult plumage also present in the nominate race.

[*Coracias*

*spatulatus spatulatus*.

Photo: Josep del Hoyo/Lynx]



Although rollers usually appear brightly coloured when perched, their most vivid patterning is concealed within the closed wing and tail. When these are opened, their true colours are revealed, as can be seen on this Indian Roller. The sudden flash of deep blue and azure when a roller takes flight can thus be quite startling. Compared to adults, the plumage of juvenile rollers is relatively dull and lacklustre. Rollers are sexually monomorphic and their seasonal plumage variation is minor.

[*Coracias benghalensis benghalensis*, Sohar, Oman. Photo: Hanne & Jens Eriksen]

ing it to veer at speed through tight angles, wheeling, twisting and turning in a woodland glade in a breathtaking display of aerodynamic perfection. The *Coracias* rollers sometimes pursue insects in the air and seem quite proficient at catching small ones, which they may even be able to deal with while airborne, but they lack the agility and turn of speed of the broad-billed rollers. Where true rollers (*Coracias*) do come into their own, aerodynamically, is in the extraordinary courtship and territorial-defence flights which give this family of birds its name. Members of the genus *Eurystomus* have proportionately rather longer wings and shorter legs than do *Coracias* rollers.

The plumage of coraciids is sleek, compressed and quite firm, unlike that of, for example, the *Strix* owls. Very few coraciiform species exhibit any degree of difference in plumage between the sexes, and rollers have none; nor do adults have any seasonal change in dress. Juveniles have plumage colours that are, on the whole, drab versions of their parents, the tans, purples and blues lacking the almost iridescent shine of adult birds. The rufous parts of the adult tend to be dull brown in the young bird, dark blues are more dusky, azure-blues greenish, and green-blues brownish; the pastel pinks or harsh puce-pinks of adults of some species are usually quite absent in the juveniles. The young of broad-billed rollers have a dusky bill, not a bright yellow or red one, and juvenile *Coracias* rollers do not have the outermost tail feathers elongated into streamers.

Streamers characterize four of the true rollers, the Abyssinian, Lilac-breasted, Racquet-tailed and Blue-bellied. The same four have the main part of the tail longer, and seemingly narrower, than is the case in other rollers. Long, streamered tails make their owners look less top-heavy and more balanced, aesthetically speaking, both when perched and in flight, but there is no obvious difference in courtship-flight performance between the streamered and the streamerless *Coracias* rollers. It is likely that streamers, rather than enhancing courtship, evolved as a species-specific recognition character. Like many bee-eaters, jacamars and other birds that spend much of their lives perching conspicuously on a treetop, the rollers twitch the tail a little for-

wards and backwards to help balance. Elongation of the tail may give some small but useful mechanical advantage to the balancing twitch. Exaggerating the length of the tail with easy-to-grow streamers and twitching the long, streamered tail may also then serve to give a more distinctive silhouette and to inform a distant roller of the bearer's identity.

In the context of species-specific recognition, it is interesting to note that, where two streamered species live sympatrically, there are sharp differences in their streamers. In West Africa, the Abyssinian Roller has very long streamers and the Blue-bellied Roller relatively short ones. In south-eastern Africa, Lilac-breasted and Racquet-tailed Rollers have streamers of the same length, but they are plain in the former and conspicuously spoon-tipped in the latter.

Coraciids have a complete moult which starts at some time during the breeding season, often towards the end of it. The primary moult is descendant, starting with the first, innermost, remex. Migratory species, before they leave the nesting grounds, generally suspend the primary moult, which is then completed in the non-breeding quarters. Some rollers also have a partial pre-breeding moult, in which they replace a variable amount of the feathers of the head, body and upperwing-coverts, but for most species such details are not available.

Juveniles moult part of their plumage when a few months old, the head, body and some wing-coverts being replaced, along with some or all of the tail feathers.

## Habitat

Most rollers inhabit the tropical regions of the Old World, whence one, the Dollarbird, has extended its breeding range north to Manchuria and south nearly to Tasmania. Another coraciid, the European Roller, has a breeding range well to the north of the tropics; both it and high-latitude populations of the Dollarbird quit the temperate zone after breeding and spend the off-season in the tropics (see Movements), in a variety of wooded habitats.



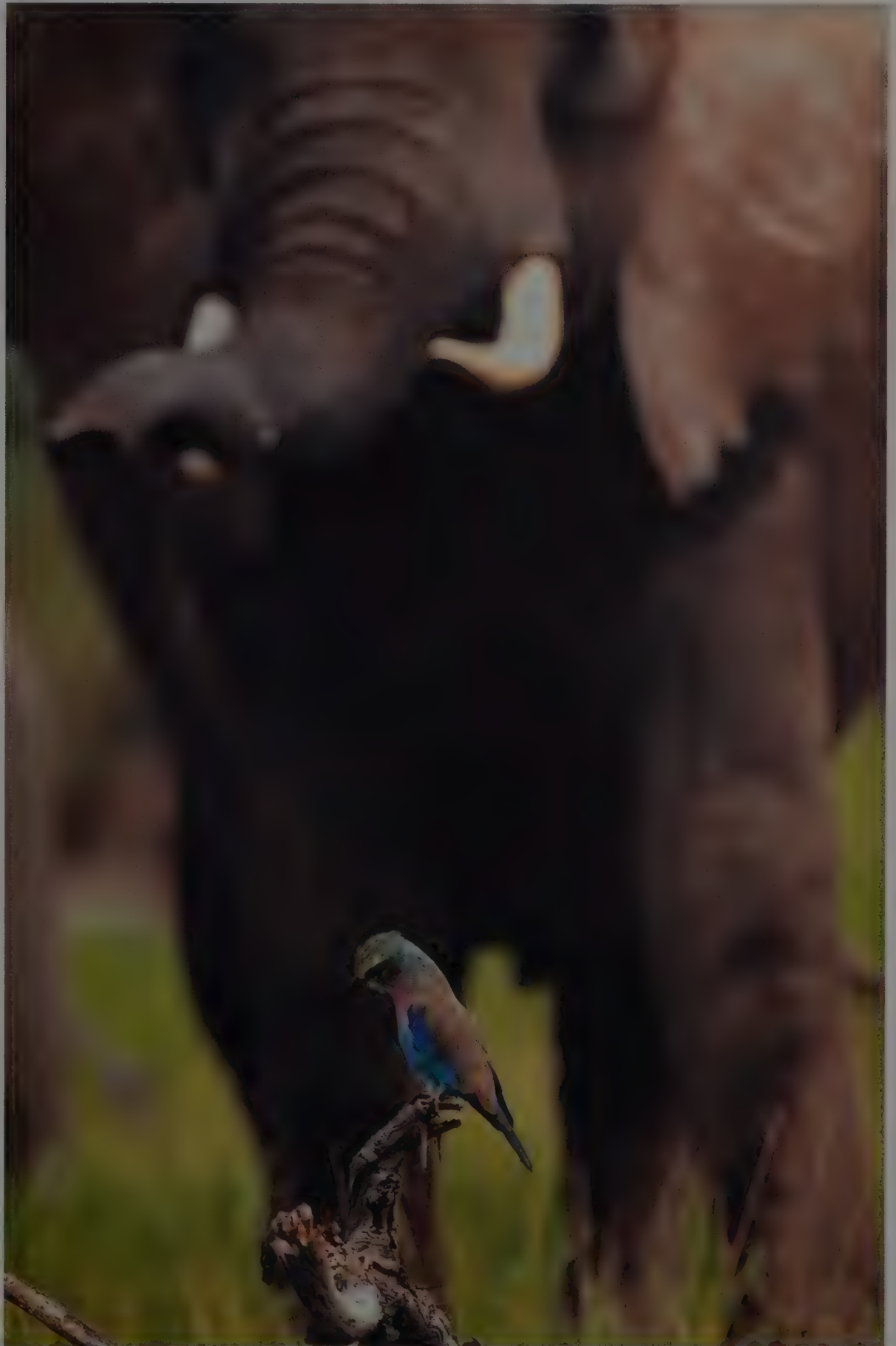
The majority of rollers inhabit the lowland tropical zone of the Old World but the fact that in terms of number of species they are most prolific in Africa suggests that it may have been in this continent that the family evolved.

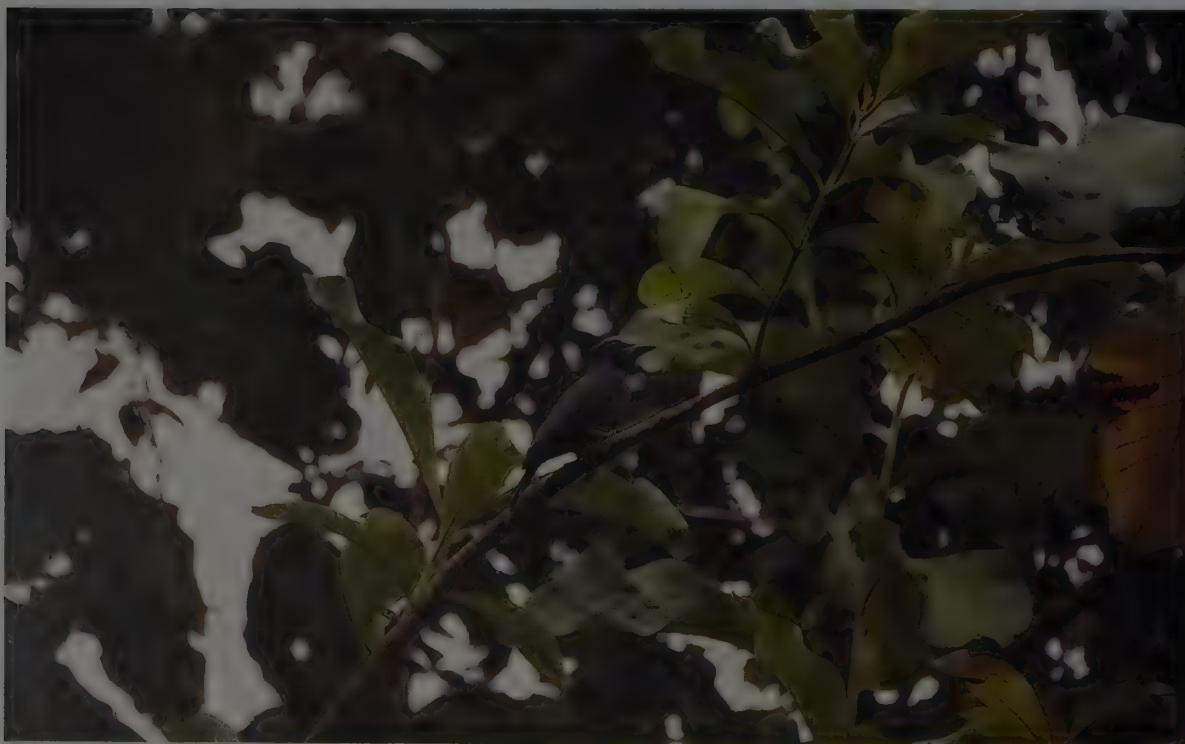
They tend to be birds of semi-open habitat, largely avoiding dense vegetation or extremely arid environments, frequenting instead more scrubby areas, savanna, dry forests and the edges of deserts and humid forests. Many occur in the African and Asian grasslands, the Lilac-breasted Roller, in particular, being a familiar sight on safaris in East Africa, where it lives

alongside large mammals such as African elephants (*Loxodonta africana*) and ungulates. Indeed, rollers regularly associate with herds of herbivores, presumably because the grazers disturb insects and reptiles, making them easier to catch. In many regions, man-made habitats such as farmland, road-sides and municipal areas have proved attractive to rollers, and as a consequence Indian (*Coracias benghalensis*) and Abyssinian Rollers (*Coracias abyssinicus*) are often found nesting in suburban buildings, and foraging happily from the artificial perches provided nearby, such as gables, lampposts and fenceposts, aerials and telephone wires.

[*Coracias caudatus caudatus*, Amboseli National Park, Kenya.

Photo: M. & C. Denis-Huot/Bios]





Only three species of roller, including the Purple-winged Roller, are associated with humid forest. This species is endemic to Sulawesi and its outliers, where it is fairly common in lightly wooded cultivation and at forest edges. It generally avoids the canopy or interior of intact forest and therefore can not be classified as a true forest inhabitant. This distinction is more accurately applied to two other species, the Azure Roller (*Eurystomus azureus*) of Halmahera and the Blue-throated Roller (*Eurystomus gularis*) of West Africa, although even these species prefer edges and clearings.

[*Coracias temminckii*, Tangkoko-Dua Saudara, north Sulawesi.  
Photo: Brian J. Coates/Lynx]

Several tropical species, inhabiting woodland, are also migratory within the tropics. On the whole, all of the migratory species utilize non-breeding habitats that are similar to their breeding ones, mainly open woodland and trees by cultivated land with some bare soil or short grass. Migrants are sometimes forced by circumstance into marginal habitats where they may have to try to find food, such habitats including desert steppe with a few low thorn bushes, or seashore dunes. Other places are entirely hostile: migrating Dollarbirds cross glaciers at 4500 m in New Guinea, and in spring European Rollers fly 600 km across the Gulf of Aden and then a further 600 km across unremitting desert in the Empty Quarter of Arabia.

Three species are closely associated with tropical lowland rainforest, and their ranges coincide with regions that are heavily forested, or were so until recently. These are the Blue-throated, Azure and Purple-winged Rollers. They live on the edges of forest, not inside it, for they all require open, uncluttered airspace in which to forage. Blue-throated Rollers often sit high in or, rather, on the canopy of rainforest, using the tops or upper sides of emergent trees and hawking above middle-height canopy to come to perch on another emergent some fifty metres or so away. To hazard a guess, the primeval habitat of the family was not closed primary rainforest, but hot, dryish, low-lying open woodland with spaced large trees over a herbaceous ground layer, thin in places, similar to that found today about 10° north and south of the equator. That is the typical habitat of Blue-bellied Rollers. These birds frequent mature, quite dense savanna woodland immediately north of the West African rainforest zone, dominated by large *Isobertlinia* trees. They avoid human habitation and seem to be commonest in old, undisturbed woodland, although they occur also along the edges of dense woods abutting grassland, marshes and even cultivation. In the southern tropics of Africa, Racquet-tailed Rollers inhabit much the same biome, little-disturbed mature savanna woodland characterized by *Brachystegia* or *Colophospermum* trees, respectively miombo and mopane woods, or *Baikiaea* or *Acacia* woodland.

All rollers are closely wedded to trees, which provide holes as nest-sites and an abundance of perches which are, for *Coracias*, at the right height above the ground or, in the case of *Eurystomus*, next to the open airspace where those species feed. Even in farmland and quite open countryside, preferred by several coraciids, rollers rest in and hunt from trees, although they commonly forage also from lookout perches on rooftops, gable ends, television

aerials, telegraph wires, standing farm machines, and similar unnatural vantage points. Being stolid birds, they appear to avoid thin twiggy perches and to prefer something firm under their feet: in trees, they tend to use branches a few centimetres thick and to shun bendy, swaying tips.

Several coraciids have exploited man-made habitats more fully. Farmland, parks and large gardens can offer excellent foraging conditions, with spaced shade trees, buildings and lamp-posts providing the hunting points, and turned earth and lawns or the open airspace above exposing grounded or airborne insect prey. In addition, old as well as ultra-modern buildings usually provide the small, dark recesses and holes that Abyssinian and Indian Rollers in particular find so attractive for nesting. It is probably true to say that, in parts of north Nigeria, east Arabia and south India, more Abyssinian or Indian Rollers nest on buildings than in trees. Both species have become thoroughly suburban birds, living close to people and exploiting houses, gardens, office blocks, parks, farmyards and fields. In Nigeria, Abyssinian Rollers belong to the Guinean and Soudanian savanna-woodland zones, but they are undoubtedly at their highest densities in such places as a large school compound a kilometre or so out of town, with teaching blocks, housing, lawns, plenty of flowering shrubs and trees, tarmac and playing fields. Indian Rollers in south-east Arabia have become as urban as Laughing Doves (*Streptopelia senegalensis*) and Common Mynas (*Acridotheres tristis*). They find nesting cavities in the roofs, eaves or sides of tall modern buildings, preferably at about third-floor level, and make free use of wires, aerials, projections, posts and garden trees as vantage points for hunting. More often than not, a pair of Indian Rollers in Oman takes over a grassy roundabout at some busy city intersection or country crossroads, nesting on the decorative architecture in the middle of the roundabout and using lamp-posts from which to search for invertebrates on the roadside grass. The same species freely uses roadside telegraph wires and farm irrigation gantries in the United Arab Emirates, and in the absence of elevated perches will sit for long periods on a stook, on a low fence, and even on the ground in stubble and hayfields where the feeding is good.

Dollarbirds have a vast geographical range and, concomitantly, they occupy a diversity of timbered habitats, recently reviewed by J. M. Forshaw. Breeding birds in Thailand, the Malay Peninsula, Sumatra, Borneo and New Guinea live in clearings and along the margins of heavy evergreen forest, and



The main link between rollers and trees lies in the birds' requirement for nesting cavities. Excavation of burrows in earth banks and use of holes in cliffs and buildings has been recorded in some species, but is the exception rather than the rule. This Purple Roller perches at the aperture of its nest-site in a large tree, and provides a clue to the habitat preferences of the family as a whole. Rollers are fairly bulky birds and, before the advent of artificial alternatives, mature trees offered the primary source of cavities sufficiently large for their reproductive purposes. As a consequence, they avoid true desert, grassland or shrubland where large trees are absent, and occur in these environments only outside the breeding season. Given their predilection for hot, dry, open habitats while foraging and their reliance on large trees for breeding, it seems reasonable to conclude that rollers probably originated in the lowland dry forests and grasslands of equatorial Africa, the miombo and mopane woodland, the semi-open and well-vegetated savannas, where tree genera such as *Adansonia* (baobabs), *Acacia*, *Brachystegia*, *Colophospermum* and *Isobertlinia* provide the requisite cavities. The association does not end here, of course, because trees also provide vital perches at varying heights above the ground to suit the foraging requirements of all rollers, with *Coracias* species tending to utilize perches at low and mid-strata while *Eurystomus* species frequent the upper canopy in order to sally out into open air-space.

[*Coracias naevius*  
*mosambicus*,  
Kaokaveld, Namibia.  
Photo: Ronald Rogoff/  
Planet Earth]







As with most tropical families, comfort behaviour in rollers is poorly documented. However, observations of several species suggest that they are very partial to sun-bathing. This Lilac-breasted Roller, for example, is adopting the typical sunning posture of birds, with wings outstretched and body feathers raised. Other species of roller have been recorded indulging in rain-bathing, during which they raised their wings to a shower when perched. The usual bathing method is to splash vigorously in puddles and pools, but flying Cinnamon Rollers (*Eurystomus glaucurus*) occasionally dive into stagnant water or even swimming pools in order to wash their plumage.

[*Coracias caudatus*.  
Photo: Kenneth W. Fink]

they forage there and just above the forest canopy; they also feed around tall mangrove, dense bamboo, old plantations of large trees, and sometimes in more open, cultivated areas where there are relict large dead trees, or in open parts of riverine swamp and *Melaleuca* forest. They are equally common in primary and secondary forest, and in the south Sulu Islands, in the extreme south-west Philippines, they seem to prefer newly deforested lowlands. Elsewhere in the Philippines, Dollarbirds inhabit forest clearings, but also timbered or even treeless grassland, from sea-level up to nearly 1250 m. In Java and New Guinea they range up to at least 1500 m and, while retaining their typical habitats, they have also colonized towns, where they live in parks, large gardens, playing fields and tree-lined streets.

Migrant Dollarbirds from the far north and south of the species' range evidently occupy the same habitats when spending the non-breeding season in equatorial and low latitudes. In China, Korea and Japan, these rollers, which are breeding summer migrants there, favour cultivated river valleys, broadleaf forest, mountainside conifer woods, open country with scattered trees at up to 1000 m, huge *Cryptomeria* trees in the gardens of old temples, and large urban green spaces, as for instance in Seoul. At the other end of their range, in northern, eastern and south-eastern Australia, where Dollarbirds are widespread breeding visitors during the southern summer, they occupy territories in rainforest clearings and *Eucalyptus* woodland, along gallery forest in valleys, in sparsely timbered grassland around swamps and lakes, in mangroves and wet sclerophyll forest, in suburban parks and gardens, and in coastal habitats.

Where two or three species of roller occur sympatrically, differences in their preferred habitat and their relative abundance are readily discernible. In Sulawesi, Dollarbirds are much scarcer than Purple-winged Rollers, and the two occur in, respectively, primary forest and secondary woodland. In West Africa, Abyssinian Rollers are commonest in suburban habitats in Soudanian and Northern Guinean woodland savanna, Blue-bellied Rollers in undisturbed *Isobertinia* woodland mainly in Southern Guinean savanna, and Purple Rollers in cultivated land with isolated large trees. In north-west Zambia, Lilac-breasted Rollers are restricted to *Burkea* savanna and partly cleared woodland and Racquet-tailed Rollers to thick *Brachystegia* woods. In many places, two resident coraciid species can be found within a kilometre of each other, yet, aggressively territorial as all breeding rollers are (see General Habits), interspecific conflict has seldom been reported.

### General Habits

The broad-billed *Eurystomus* rollers patrol their territories by flying above the trees and calling stridently and repeatedly, but they do not roll. Birds of the genus *Coracias* are the only true "rollers", and in many regions their dramatic, noisy, rolling flight displays can be seen almost throughout the year. Until recently these displays might have been regarded as manifestations of

The Purple Roller, like other rollers, has a rather restricted vocabulary, consisting almost entirely of harsh, strident monosyllables. These are given frequently when perched, often as contact calls, in alarm or in response to territorial intrusions. The most impressive vocalization is given by male *Coracias* rollers during display. These high-speed flights, in which the bird's body swivels rapidly from side to side while its head is kept level, are accompanied by an accelerating volley of loud rasping calls.

[*Coracias naevius mosambicus*,  
Nylsvley, South Africa.  
Photo: Warwick Tarboton]





Like its congeners, the Lilac-breasted Roller is a sit-and-wait predator that surveys open foraging habitat from a prominent perch. Favoured look-out posts are generally bare branches, wires or posts 1-6 m above ground from which an unobstructed view of the surrounding terrain is available. Rollers are archetypal sun-loving birds that appear to be little affected by high temperatures, standing sentinel for long periods during the heat of the day, sometimes waiting at a particular perch for long periods without moving until suitable prey comes into view.

[*Coracias*  
*caudatus caudatus*,  
Chobe National  
Park, Botswana.  
Photo: Günter Ziesler]



general, social behaviour, rather than particularly sexual behaviour. Studies of Abyssinian Rollers by G. Balança and M. N. de Visscher, conducted in Burkina Faso in the early 1990's, have shown that there is, as would be expected, a major reproductive component in the displays, but that there is also a later period of intense display activity which evidently has quite a different function. Those authors' main observations and inferences are as follows.

"Rolling" display-flights are aggressive, and are often clearly directed at an interloper such as a human being. In typical rolling display, an Abyssinian Roller flies up high, tilts forwards, and accelerates in a long, slanting dive to within a few metres of the ground, at first beating its wings powerfully and then, as it picks up speed, rocketing along with the head not rotating but the trunk and flaying wings rolling through perhaps 270°, clockwise and anticlockwise, around the bird's axis and flightpath several times per second. Shrieking, and hurtling towards the ground, the bird abruptly stops rolling and levels out, and then, slowing down, it flies up high and repeats the process, often several times. Rolling flights are performed most often during the second half of June, in the Burkina Faso study area, when a pair or trio of birds is installing or reinstalling itself in a tree-hole nest, and eggs are being laid. Also in June, greeting ceremonies and courtship feeding are commonplace. Rolling behaviour is at that time doubtless connected with social advertising, bonding and territory establishment, and in that sense is a reproductive, agonistic behaviour. There follows a lull of three months, during which time the young have flown, the annual rains have come and gone, and part of the Abyssinian Roller population has migrated southwards. In October and November, the migrants return to the area and to their nesting trees, evidently displacing the few rollers that had remained in, or entered, the study area, and they quite markedly resume their rolling displays. Forshaw has noted that, in Australia, Dollarbirds also are noisy and showy in the air up to the time of egg-laying, but then become silent and wary, until later, when the young are fledging, they are spectacularly aggressive once more.

Other forms of aggressive behaviour of Abyssinian Rollers, such as bickering and the chasing away of interlopers, are evident during the nesting season, but barely at all in August, when

the young are on the wing. Again, however, aggression becomes far more frequent from late September until early November. All sorts of birds, from raptors and shrikes (Laniidae) to crows, hornbills and turacos (Musophagidae), are chased away from the rollers' territories, and it is notable that hole-nesting species are the main victims. Abyssinian Rollers are themselves harried by the even more aggressive Cinnamon Rollers, although near their nest trees they seem to give as good as they get. By far the greatest amount of aggression by Abyssinian Rollers is directed at their own species, however, around the nesting trees from late September to November. This behaviour is thought to be a stratagem for survival: severe intraspecific competition apparently exists for a productive parcel of land to sustain the pair during the coming non-breeding dry season,

When appropriate prey is detected, *Coracias* rollers usually watch intently for a couple of seconds before dropping from their perch, flapping their wings once or twice, then gliding, sometimes over considerable distances, to pounce on their terrestrial quarry. Their wings are spread open as they alight, often with a vivid flash of colour, as shown by this Indian Roller, and the prey is instantaneously seized with the bill.

[*Coracias benghalensis*  
*benghalensis*,  
Sohar, Oman.  
Photo: Hanne &  
Jens Eriksen/Aquila]





Although the standard hunting technique of the *Coracias* rollers is sit-and-wait, they will also at times use a variety of other methods, many of them of a rather more aerial nature. The European Roller frequently forages in flight in a manner reminiscent of swallows and martins (*Hirundinidae*), at which times it regularly consumes its aerial prey while airborne, without pausing on a perch. At times, in its African winter quarters, it can be seen flying back and forth through clouds of swarming termites, pausing only from time to time on a perch; similar treatment may be used with swarming locusts. Also, on occasion, this species will hover and then drop to take prey on the ground, although in a sense this is more closely equivalent to the sit-and-wait technique, effectively using a non-existent aerial perch.

[*Coracias garrulus garrulus*, Nava del Rey, Valladolid, Spain. Photo: Javier Echevarri]

and to provide a territory containing suitable nesting trees for the subsequent breeding season.

If rolling displays and other aggressive types of behaviour were restricted to the few weeks around the start of nesting, there might be little call for comment. It is all too easy to suppose that the breeding season begins shortly before eggs are laid; but, if we think of the Abyssinian Roller's season as commencing in autumn, seven months before the species lays, the dual peaks of its aggressive behaviour are easier to interpret. In autumn, the short-term rainy-season emigrants return from the south to their breeding grounds, displace others of their species, assert their dominance over inexperienced yearlings, seek a mate or bond anew with the previous season's mate, and establish a "winter" territory. It is therefore in the autumn that the most intensive agonistic behaviour of the year is seen. If the pair survives the harsh non-breeding dry season, there will be further pair-bonding, territorial and nest-ownership activities in the spring, though less intensive than in the autumn. Two other roller species that are known to form or re-form pairs well before egg-laying are the Indian and European Rollers, and there is evidence that individuals of the latter pair up on their African wintering grounds.

Besides their screeching and rolling aerial dives, which might be used not only to frighten away people and ground predators but also to attract a mate and to intimidate a rival, several *Coracias*

rollers have what seems to be a territorial patrol-flight. An Indian Roller in Oman once flew in a wide circle, high over buildings in a university campus, calling continuously. Its flight lasted 48 seconds, and was slightly undulating and once or twice semi-rolling. Such flights frequently end with the bird accelerating downwards at a shallow angle, shrieking raucously, rocking fast from left to right around its body axis, and often striking a terrestrial interloper such as a person, a dog or a fox (*Vulpes*).

There is an additional complication in the social lives of *Coracias* rollers: in some species, non-breeding individuals are tolerated by a breeding pair in its territory. In June, Balança and de Visscher studied Abyssinian Rollers intensively on a 2-ha patch of ground with a dozen large baobabs (*Adansonia*), a favourite nesting tree. At first, seven birds were interacting aggressively, and several of them tried to enter a hole in one of the baobabs, where there was protracted scrapping. Eight days later, only three birds occupied the tree, quite amicably, and one of them was evidently incubating eggs. Elsewhere, three rollers lived on and around a baobab where two of them were feeding young in a nest-hole.

A third bird may associate with a pair of European Rollers, although that observation requires confirmation, and it is certainly not established that any third bird is a helper in the sense applied to, for instance, some bee-eaters of the genus *Merops*. J.



M. Thiollay studied Blue-bellied Rollers in Ivory Coast and found that they live all year in small, cohesive groups of three to seven birds, sometimes more, and once as many as 20. Members of a group keep quite close together, and certainly within sight and sound of one another for most of the time, flying from tree to tree and foraging through a jointly defended territory more or less together, all indulging in a bout of preening about the same time, and roosting at night as a group in the same tree. Unfortunately, he was unable to establish the reproductive roles, if any, of supernumerary individuals, because of the inaccessibility of nesting-holes high up in palms and trees. There remains the strong expectation, however, that the Blue-bellied Roller will prove to be a co-operative breeding species, with a social organization perhaps similar to that of one of the co-operative breeding bee-eater species, or to that of woodhoopoes of the genus *Phoeniculus*.

Much more needs to be known about the demographic and social structure of all rollers. Before their habits can be interpreted and the adaptive natures of their societies understood, a great deal of study and research is required with regard to their displacements, longevity, mortality, the numbers of non-breeding birds present in the breeding season, breeding success, and the incidence and meaning of co-operative breeding.

Indian Rollers drink at a puddle or dripping tap, and their congeners probably do likewise. *Eurystomus* rollers, however, sometimes drink by flying in a straight line low over the still surface of a large pond, the mandible cutting the water a few times, like some giant swallow (*Hirundinidae*).

Sun-bathing is common among those coraciids that have been sufficiently well studied. The Indian Roller, for example, frequently indulges in this behaviour, spreading its wings fully to absorb the warmth of the sun's rays. That species has also been recorded rain-bathing: the birds were perched on a wire, and adopted a striking posture with the wings raised over the back. The European Roller and the Dollarbird, too, have been observed rain-bathing, and it seems likely that other members of the family exhibit this and similar comfort behaviour, although, for many, information is lacking. Cinnamon Rollers appear to be particularly fond of bathing, by plunging into water from a perch; they have even been known to dive into a swimming pool for this purpose.

## Voice

One of the several ways in which *Coracias* rollers recall crows and their allies (*Corvidae*), an entirely unrelated family, is vocally. The *Coracias* species make harsh, strident, cawing noises, and none of them has any redeeming euphony or diversity of sounds to speak of. In his review of the voice of the European Roller, M. G. Wilson transliterates some contact-alarm calls as "cruk", "kack", a wooden "kack-ack", and a "caw" like that of a Rook (*Corvus frugilegus*) but higher-pitched; the warning call he transcribes as a loud screeching "aaaaaaarrrr", recalling a Eurasian Jay (*Garrulus glandarius*), and a call given when a roller is attacking or repelling intruders as "k-k-k-k-k-k-rak-ra" or a rattling "prrra-prrra-prrraaa" like a Black-billed Magpie (*Pica pica*).

Calls are uttered equally at the perch and on the wing. Bearing in mind the sizes of these birds, their voices are moderately loud, and they are louder still in the accelerando and crescendo of rasping "raak" notes when the bird is flying at its fastest in the middle of its rolling display (see General Habits). In its advertising display-flight, a European Roller climbs quite high into the air, tilts forwards and starts to call, quietly at first, with clucking notes uttered regularly at four to five per second. Still calling, the bird flies faster, and the "kuk" notes gradually become louder, longer and slower, which gives the noise an attention-demanding, menacing and, to a human observer, often frightening quality. By this time the roller's dashing descent is levelling off, fast rolling has developed, and the "kraak" calls have accelerated through a sound like the winding of a football fan's rattle into a loud and intimidating confusion of "kraasch" sounds. Other *Coracias* rollers have similar voices.

The voices of these birds carry well through the open woodland that is the preferred habitat of most rollers. A sharp-eared listener can readily hear most calls of a perched roller at about 100 m, and the display-flight "kuk" and "kraasch" notes at about 300-400 m or more, depending upon conditions. Doubtless the birds themselves can hear each other at these distances, and probably from farther away. All rollers are vocal during all daylight hours, and even a perched Indian Roller, unmoving and seemingly drowsy during the hottest hour after noon, will give a quiet "kruk" every ten or fifteen minutes.

The Purple Roller, like many of its congeners, sometimes captures dangerous prey items such as sizeable scorpions. It deals with these boldly and promptly, dealing them rapid blows and crushing them quickly after capture. In addition, rollers consume a surprising quantity of distasteful or poisonous insect and non-insect invertebrates that are generally avoided by other predators. These include caterpillars of the goat moth (*Cossus cossus*) and a multitude of noxious beetles and sinister centipedes.

[*Coracias naevius mosambicus*, Ghanzi, Botswana.  
Photo: Peter Johnson/  
Corbis]





The prey of Coracias rollers generally consists of large invertebrates, rarely smaller than 10 mm in length, and small vertebrates. Insects predominate in the diet, amongst which beetles (Coleoptera, especially rather large and hard-shelled varieties) and crickets (Orthoptera) tend to be the most frequently eaten, along with smaller numbers of earwigs (Dermaptera), preying mantises (Mantidae), as well as adult and larval butterflies and moths (Lepidoptera), flies (Diptera) and many other groups, depending on the region. Indeed, rollers appear to select prey merely on the basis of size and availability, rather than any more specific preference. Insects are by no means the only prey targeted: almost anything in the appropriate size bracket that happens to wander into range is liable to become roller food. For example, spiders and scorpions (Arachnida), snails and slugs (Gastropoda) and earthworms (Annelida) have appeared on the menu, while the list of vertebrates consumed includes tadpoles, frogs (as in the case of this Lilac-breasted Roller), a variety of reptiles and even, occasionally, small mammals and birds. The latter are generally only taken when very young, but small exhausted migrants have occasionally been captured after making landfall on Mediterranean islands. In certain species, this insectivorous and carnivorous diet is supplemented by ■ small quantity of fruit, such as figs (Ficus) and grapes (Vitis).

[*Coracias caudatus*  
caudatus,  
Botswana.  
Photo: Hilary Pooley/  
Oxford Scientific Films]



Even when tackling large prey items, the Lilac-breasted Roller swallows them whole, and this is a feature of the feeding technique of all members of the family.

All rollers crush prey in their bills after capture, sometimes adding a brief beating on a hard surface to soften or subdue it, but they never dismember it. Most items are dispatched and consumed in a matter of a few seconds, though occasionally the process can take somewhat longer. Indeed, on one occasion a Lilac-breasted Roller was recorded taking over eight minutes to swallow a frog.

[*Coracias*

*caudatus caudatus*,  
Masai Mara, Kenya.

Photo: M. & C. Denis-Huot/  
Bios]



An Indian Roller in Oman, when performing an apparent territorial patrol-flight lasting 48 seconds (see General Habits), gave 120 monosyllabic call notes at regular intervals of 0.3-0.5 seconds. These sounded like "kaarsch" when the bird was nearly rolling, but "chak", like a Eurasian Jackdaw (*Corvus monedula*), in airy level flight. At its farthest point the roller was about 500 m from the observer, yet its "chak" calls could easily be heard.

The rollers of the genus *Eurystomus* have an even more limited vocabulary than the *Coracias* species. At a perch, as well as in territorial flight above the trees, Blue-throated Rollers make shrill, monosyllabic, repeated squawks, Cinnamon Rollers emit bouts of guttural vowel sounds such as "(g)iaow, grrd, grd-grrd, g r g" and a long rattling "g r r r r r r d", while Dollarbirds call "kek, kek" at perch and have a strident, crescendo "kek...kek...kek-kek-kek-kek-k-k-k-k" contact and territorial call.

### Food and Feeding

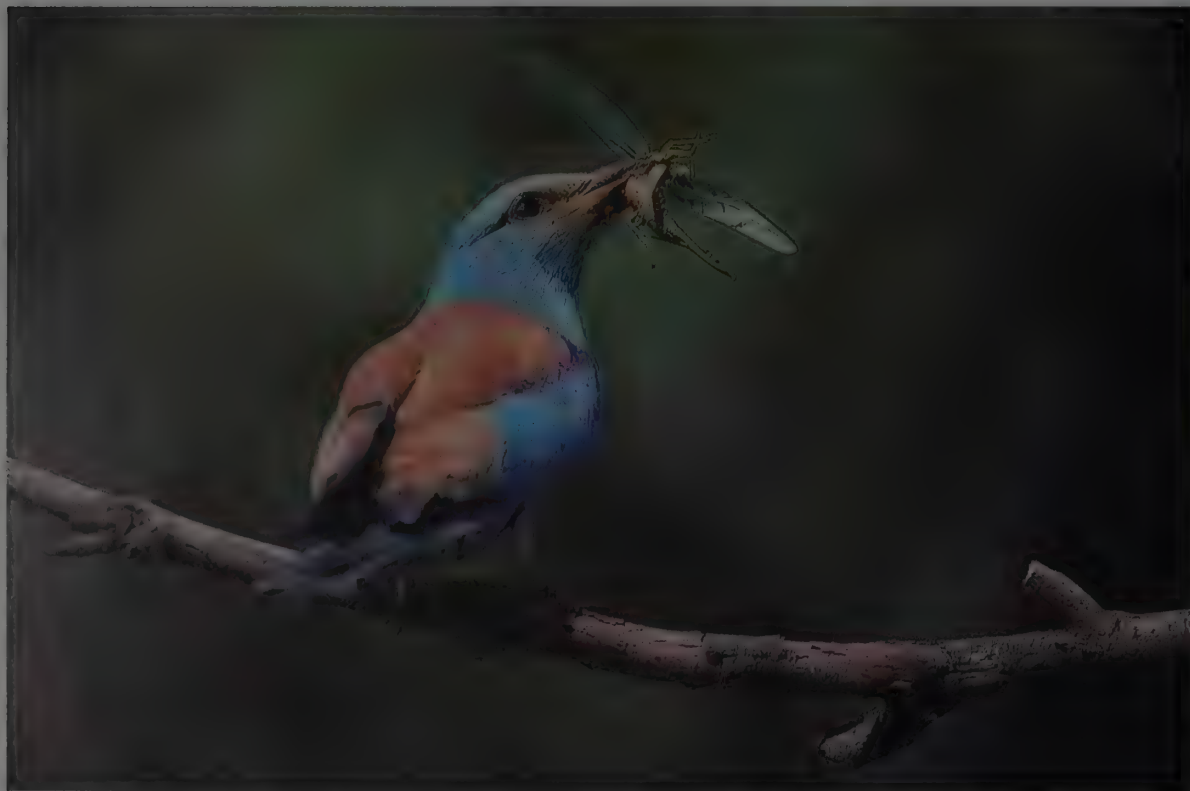
Alike as the two coraciid genera are in size, shape, plumage and general morphology, except for the bill, and similar though their diets may be, their foraging techniques are sufficiently different to warrant separate discussion.

The members of the generalist genus, *Coracias*, are sit-and-wait predators. That is to say that, instead of actively seeking out and pursuing their intended food, they choose a perch from which they have a more or less unobstructed view of the ground below and within a radius of 10 m or more, and there they sit with apparent patience until a suitably sized animal may appear. They are very much hot-climate birds, and seem to be not in the least bit discomfited by burning midday temperatures, nor by perching in the open under a cloudless sky. "Patience" may not be an appropriate term to apply to a sit-and-wait predator; in fact, after a fruitless wait of an hour or so at a particular perch, the bird, having not

fed, will fly to another perch and try there. Often a roller will change perches every few minutes, and to that extent it could be said to be impatiently searching a lot of ground for food, much as a continuously flying swallow covers a lot of airspace.

The eight species of *Coracias* have been studied to very variable extents, but so far as is known they all have much the same foraging behaviour and diets. They are predators of insects, particularly larger beetles and grasshoppers, and of other invertebrates such as scorpions, and a range of small vertebrates. Much is known about the food and feeding biology of the European Roller, which has been reviewed by Wilson. In one study of more than 2200 prey items, nearly half measured 10-15 mm in length and a further 40% were 15-30 mm long. Like most insectivorous birds, rollers regurgitate neat and well-formed blackish pellets containing the undigested chitinous parts of the insects' exoskeleton. A roller ejects up to a dozen pellets during the day and one or two more during the night. These pellets are up to 10-15 mm wide and twice as long, each one containing the remnants of some 15-24 insects, and they have proved to be a useful source of information about the diets of both young and adults. Partly from pellet analysis, it has been shown that the predominant prey items of European Rollers are those insects longer than 10 mm which are the most abundant on the surface of the ground. It seems, therefore, that rollers select food according to its size, but that, within that constraint, they eat whatever is available.

On the lookout for food at a perch some 3-6 m above open ground, a roller turns its head or slightly shifts its footing from time to time, although it does not have the alert, constant head-turning and head-tilting, ready-to-go appearance of, for instance, a bee-eater. When an insect is spotted, the roller peers down at it and may take a few seconds before launching itself downwards, as if gauging the situation. Then the bird drops, perhaps flapping its wings once or twice, and glides down, more often at a shallow angle than steeply, alights next to the victim and grabs it with the



bill, or pursues it with clumsy hops for a second or two. The whole sequence, from inspection to launching, gliding down, folding the wings, and seizing the prey, looks unhurried, although not, perhaps, imprecise. As often as not an Indian Roller deals with its prey on the spot, but European Rollers generally fly back to a perch carrying the prey in the bill. At the perch, the victim is crushed in the beak and beaten a few times against the branch, perhaps tossed just clear, and then swallowed whole. Insects'

legs and wings are not removed, although they sometimes fall off. A mouse (Muridae) may be subjected to shaking as well as beating. An Indian Roller once took some 20 seconds to kill a mouse, then twice as long to engulf it, head first, when the bird looked like a young owl, half asphyxiated during the process.

As might be expected of a somewhat unselective, generalist feeder, the list of prey items of the relatively well-known European Roller is lengthy. Beetles and crickets and their relatives

Some roller species tend to deal with prey on the ground. Others carry food items back to a perch where they are manipulated before consumption, as is the case of this European Roller with its bush-cricket prey. Insect prey is often tossed slightly into the air and recaptured to position it in the bill, a trick practised by young rollers with pebbles and lumps of earth. Partly because they devour prey items in their entirety, rollers must eject their indigestible portions at regular intervals. Accordingly, up to a dozen occasions through the day and once or twice through the night, rollers regurgitate blackish pellets, neatly parcelled fragments of the chitinous exoskeletons of insects.

[*Coracias garrulus*.  
Photo: Roland Mayr/  
Oxford Scientific Films]



The European Roller and several other *Coracias* species are quite prepared to tackle snakes. They tend to limit themselves to smaller snakes, usually measuring less than about 20 cm in length, although, as with their foraging strategy in general, they appear to be somewhat adaptable. Once snatched, the snake is rapidly crushed and beaten to death, essential processes in order to ensure that the bird itself suffers no injuries. This Horseshoe Whip-snake (*Coluber hippocrepis*) appears to be in its last throes.

[*Coracias garrulus*  
*garrulus*,  
Cañada de las Norias,  
Almería, Spain.  
Photo: José Bayo Valdivia]



The characteristic and spectacular rolling flights undertaken by male *Coracias* rollers possibly serve a territorial function and the extent to which they are sexual in nature remains to be determined. These Indian Rollers are performing another type of display which often involves bowing and allopreening, followed by a jerking of the bills upward, with tails fanned and wings slightly drooped, and chattering in unison. This behaviour often precedes copulation and presumably functions in pair cohesion. Another similar type of display, given when pair or family members meet, is called a "palaver".

[*Coracias benghalensis*  
*benghalensis*,  
Corbett National  
Park, India.  
Photo: Otto Pfister]

are favoured everywhere, and include the following: tiger and ground beetles (Carabidae), burying and rove beetles (Silphidae, Staphylinidae), gold-beetles (Buprestidae), stags (Lucanidae), scarabs and chafers (Scarabacidae), click beetles (Elateridae), flour beetles (Tenebrionidae), ladybirds (Coccinellidae), longicorns or longhorns (Cerambycidae), leaf beetles (Chrysomelidae), weevils (Curculionidae), diving and silver beetles (Dytiscidae, Hydrophilidae), crickets (Gryllidae), long-horned and short-horned grasshoppers or bush-crickets (Tettigoniidae, Acrididae), mole-crickets (Gryllotalpidae), mantises (Mantidae), cicadas (Cicadidae) and many families of plant-bugs (Hemiptera), earwigs (Dermaptera), butterflies (Vanessidae, Pieridae) and caterpillars of hawkmoths (Sphingidae) and noctuids (Noctuidae), ants, bees, wasps and sawfly larvae (Hymenoptera), termites (Isoptera), and adult and larval flies (Diptera) of many families. Other arthropods, eaten uncommonly by European Rollers in Europe but frequently by them and other rollers in the tropics, include spiders, millipedes, centipedes, scorpions, pseudoscorpions and solifugids (Solifugidae). Snails, slugs, mussels and earthworms have been recorded in diets, and vertebrates include tadpoles, small frogs, fish fry, lizards, slow-worms (*Anguis*) and snakes up to about 35 cm long, mice and shrews, and nestlings of birds and, occasionally, exhausted adult migrant birds.

Numerous analyses of the diets of adult European Rollers, and of nestlings, conducted mainly in the former USSR, have involved hundreds of pellets or stomach contents and thousands of food items. They have shown that food given to nestlings is much like that consumed by the adults themselves, and that there are considerable regional and temporal differences in diet composition.

While watching from a perch for arthropods on the ground is by far the commonest foraging option for the European Roller, this and other *Coracias* species sometimes employ other techniques, too. Rollers are known to fly-catch from an elevated perch, and in Arabia Indian Rollers often sit on a lump of earth or a pile of straw in a stubble field and fly up to give short chase to airborne grasshoppers. How efficient that stratagem may be has not been determined, although there is no doubt that it quite often results in successful captures. Indian Rollers fly animatedly behind and around haymaking tractors, snatching up small grasshoppers on the wing, or hovering momentarily before dropping on to an insect on the grass. They follow the cutters so closely,



like gulls (*Larus*) behind the plough, that a bird is not infrequently caught up and killed.

European Rollers have been seen following the plough, and also in sustained hunting flight, like a swallow. Again, it is hard to know how successful they are. This is partly because they do not necessarily come to a perch to deal with a capture, when it would be easy to see that a capture had in fact been made, but they may eat the items, presumably only small, easily dealt-with ones, in the

Rollers engage in vigorous disputes centred around territorial defence.

There appear to be two peaks of aggression in the Abyssinian Roller: one from about late September to November, when birds that had migrated south have just returned to the breeding grounds, and are thus re-establishing territories; and the other shortly before egg-laying, generally around March. In most cases, territorial disputes are settled merely by threats, the intruder abandoning fairly quickly, but on occasion the two birds come to close quarters and may actually become interlocked.

[*Coracias abyssinicus*,  
Burkina Faso.  
Photo: Jacques Gilliéron]





A male Lilac-breasted Roller tosses a large beetle into the air to reposition it in his bill, then transfers it to his mate, who performs the same movement before consuming the item. The provisioning of females by males, termed courtship feeding, is frequent in many coraciiform and piciform groups such as the bee-eaters (Meropidae) and jacamars (Galbulidae). In general, it is a feature of early pairing behaviour, the period immediately prior to and during egg-laying and, to a lesser extent, the incubation period. It is thought to function partly as an additional food supply for females when their energetic requirements are exacting. Courtship feeding in rollers has been recorded throughout the breeding cycle, even during chick provisioning and after fledging, but is at its most frequent during the laying period, and in some instances almost all the female's food supply is thought to have derived from the male at this time. Considerable evidence in other bird families suggests that males signal their quality, or the quality of their territory, through high courtship feeding rates, and that females prefer males that provide more food. Whether this is the case in rollers remains to be determined. Interestingly, courtship feeding in European Rollers (*Coracias garrulus*) has been noted more commonly in the African wintering grounds than in the temperate breeding grounds, prompting the suggestion that pairing commences in advance of, or during, their northward migration.

[*Coracias caudatus caudatus*, Samburu Game Reserve, Kenya. Photos: M. & C. Denis-Huot/Bios]



Repeated mating usually takes place on a perch near the nest-site, from around a week prior to egg-laying until the deposition of the last egg. In these copulating Indian Rollers, the female is clearly seen holding a large insect in her bill, a fact that strongly suggests that the male's successful advances were preceded by a gift of food. In many bird species courtship feeding is a regular precursor to copulation and this appears to be true, at least on occasion, in rollers. The pair members usually sit in close proximity on the perch, performing relatively brief courtship displays that include allopreening, chattering and food provisioning, behaviour that may then culminate in copulation.

[*Coracias benghalensis benghalensis*, Keoladeo National Park, Bharatpur, India.  
Photo: Manfred Pfefferle]



air. There are observations of rollers in flight gleaning insects from the tops of standing cereals, fluttering but not alighting. In Africa, when a European Roller comes to a hatch of termites or ants, it snatches up the alate insects from the air one at a time. Such prey items are small and soft, and the roller swallows each one as it catches it. At a hatch of flying termites the bird does perch often, but the purpose of perching, at least in the case of the Abyssinian Roller, is not to enable the roller to beat a capture against the branch but, rather, to rest momentarily, or perhaps to gauge which course next to fly along with a resting or turn-around perch at the far end.

Like all *Coracias* rollers except the Blue-bellied, Abyssinian Rollers forage essentially solitarily. Nevertheless, several will attend a herd of antelopes to feed upon insects that are put to flight from the grass, and up to 20 may congregate at a bush fire, where they hunt actively from perches or in sustained flight. Hornbills, drongos (*Dicrurus*), bee-eaters, and other rollers are regularly attracted to grass and bush fires; Indian Rollers attend them regularly, and have acquired several local names because of this association (see Relationship with Man). In Oman, Indian Rollers sometimes feed after dark by sitting on a street lamp and dropping down for grounded insects that have been attracted to the light; they also scavenge such items as scorpions run over by cars on the road, and they quickly move on to a newly made lawn to exploit beetles on it and beetle larvae in it.

As predators, rollers are essentially opportunistic. Presumably, sit-and-wait foraging generally suffices to provide them with their daily needs, but they may readily learn that insects can be had by other hunting techniques at a fire or on the farm, and they will employ those techniques as opportunity affords. They have to compete for much of their insect diet with numerous other insectivorous birds; but not many others are strong enough to tackle the quite large and often very hard-shelled beetles that are the rollers' mainstay. Moreover, rollers eat a lot of distasteful and toxic or even highly poisonous items, so they may be at an

advantage over many of their competitors in having more powerful digestive and more versatile detoxifying systems. Examples of prey taken by European Rollers, but avoided by most other birds as distasteful or dangerous, are the beetles *Procrustes coriaceus*, *Calosoma sycophanta* and *Lampyrus noctiluca*, caterpillars of the goat moth (*Cossus cossus*), the widespread African grasshopper *Zonocerus elegans*, centipedes, scorpions, solifugids, and shrews. Tropical rollers seem to eat a lot of scorpions, seizing them boldly and quickly crushing and beating them. Such behaviour is common and well documented for the Indian Roller.

European Rollers quite commonly consume grapes in the Ukraine and figs in the Mediterranean, and there are a few records of their taking other fruits from time to time. In Ivory Coast, Blue-bellied Rollers sometimes consume whole fruits of oil palms (*Elaeis guineensis*).

Aerial hunting is the usual means of feeding in the genus *Eurystomus*, and it can be thought of as a specialism grafted on to the primitive roller option of sentinel-feeding, the sit-and-wait technique from an elevated-perch. A nice example of opportunism and learning by Dollarbirds in Sarawak was recounted by Forshaw, citing J. E. Duckett. Every day, up to eleven of the rollers assembled, together with other aerial insectivores, to snap up live cicadas caught by a villager the previous night and released one by one into the air. Dollarbirds and Blue-throated Rollers forage on occasion by scanning from a high perch and flying down to the ground for a mouse or beetle, much in the manner of a *Coracias* roller except that, on the ground, *Eurystomus* rollers, with their shorter legs, are even more inept at giving chase. As evidence that Cinnamon Rollers come to the ground, spiders have been found in stomachs of specimens taken in Africa and mollusc shells in others from Madagascar; the latter are not food but are gastroliths, ingested into the gizzard to help it to fragment hard insects. Ground-feeding, however, is unimportant among these birds, and Cinnamon Rollers are in fact almost exclusively aerial.



Recent findings indicate that there is still a great deal to be learnt about even the best known of the roller species, the European Roller. The male bird emerging from this nest-hole in an almond tree carries in its bill the shattered remains of the first egg laid by his partner. The pair went on to consume the egg between them, a process which the photographer witnessed on several other occasions involving different pairs. Below, the male offers eggshell to his mate as a form of courtship feeding. It may be that at this crucial stage in the breeding process the female sometimes requires ■ boost to her calcium intake, in order to produce ■ stronger, tougher shell for her clutch. What is not yet known in these instances is whether or not the first egg was broken accidentally, or whether the adults possibly realized somehow that the female's calcium levels might temporarily be insufficient for production of a full, healthy clutch. For the moment, all this remains a matter for speculation, and further research is clearly called for.

[*Coracias garrulus garrulus*, Nava del Rey, Valladolid, Spain. Photos: Javier Echevarri]



Largely because of the inaccessibility of their nests, very little is known about the reproductive biology of most members of the family, the exception being the European Roller. In common with all its relatives, this species generally occupies arboreal nest cavities, sometimes with a few twigs or dead leaves as a rudimentary lining; in this hole two to six white eggs are laid at roughly two-day intervals. Cavities are either natural or the result of woodpecker (Picidae) excavation. The species has also been observed nesting in holes in new or abandoned buildings, in cliffs, and even excavating its own burrows in loamy earth banks in Pakistan. Both parents contribute approximately equally to diurnal incubation, although only the female incubates at night.

[*Coracias garrulus garrulus*, Toledo, Spain.  
Photo: Miguel Angel de la Cruz]



The foraging behaviour of the Cinnamon and Blue-throated Rollers has been studied in Ivory Coast by Thiollay, and is of exceptional interest. For the greater part of the day, solitary birds and pairs perch conspicuously on a dead branch up to 30 or even 40 m high in woodland, or at the top of a tall tree above the forest canopy, where they have a clear view all around them. Blue-throated Rollers launch themselves out from time to time to catch a passing insect, but Cinnamon Rollers scarcely feed at all before 17:00 hours, unless a swarm of winged termites rising up through the canopy proves too much of a temptation. Both species defend the airspace around their perching points with vigour, and against all intruders, not only other rollers but also hornbills, hawks (Accipitridae), parrots (Psittacidae), crows, and similar-sized birds in the tops of the trees or above them. Calling the while, the roller flies after the intruder and sees it off. Cinnamon Rollers, which bother to catch an insect only once an hour or even once every three hours between dawn and late afternoon, are particularly aggressive and give chase to other birds many times and for considerable distances.

Late in the afternoon the rollers become restless, and then fly away in search of the swarming hatches of flying ants and termites that are such a daily feature of life in the humid tropics. Rollers of both species congregate at an insect swarm of good-sized termites or ants, such as *Macrotermes* or *Crematogaster*, and prey on them in a sort of feeding frenzy. Commonly, five or ten birds forage together in graceful, buoyant, powerful and erratic wheeling flight, swooping in fast, straight or curving glides around and above the treetops and, in large clearings, almost down to the surface of the ground. As many as 280 rollers have been counted at a time, and in steadily failing light the two species sweep silently through the air, ignoring each other and the swifts (Apodidae) and swallows that often exploit the same swarms, intent only on catching as many insects as they can before they are overtaken by nightfall. One bird catches an insect in its wide bill every six to ten seconds, and the prey is crushed and eaten in flight without pause, much as a swift feeds. Hunting well into the late dusk, the rollers gorge themselves on hundreds of insects.

The stomachs of two Cinnamon Rollers, taken at nightfall, contained, respectively, 714 and 748 insects totalling 37 g and 39 g in weight, or about 40% of the bird's body weight.

Taking all of the daily requirement of food in such a short period as an hour or two is unusual among bird species. In some tropical-forest frugivores such as manakins (Pipridae), for instance, the spare time has contributed to the evolution of bizarre social rituals and mating systems. In the dry season, however, and at other times when insects are not emerging in swarms, *Eurystomus* rollers forage more like the *Coracias* species: all day long and upon such prey as can be had. Further study may yet reveal that all is not entirely orthodox in roller sociobiology.

## Breeding

True to the habits of the order to which they belong, the rollers are hole-nesters and, like all coraciiform and some other cavity-nesting birds, they lay white, subspherical eggs. The eggs are white, it is generally argued, to make them more visible in often dark cavities to the incoming parent, and rounded because there is no adaptive reason for them to be otherwise. Round eggs in a good-sized clutch fit together well beneath the incubating bird, and in a deep cavity they do not have to be pointed, like the eggs of ledge-nesters, to roll in tight circles for reasons of safety.

Most other families of coraciiform birds utilize holes in the ground, burrows which the birds generally dig for the purpose. Rollers, however, like the barbets and the woodpeckers and most other piciform families, nest in elevated holes. Tree holes are used by all rollers, several species breeding also in crevices in cliff faces and cavities in buildings, and old woodpecker or starling (Sturnidae) holes are often used. Such sites are only to be expected in a family that is so closely wedded to trees for their abundant provision of sentinel-foraging perches and one that is so prone to capitalize on the feeding opportunities afforded around human habitation. In contrast, European Rollers in Pakistan sometimes excavate burrows 60 cm long in loess earthen banks.

The most remarkable aspect of breeding is the spectacular, rolling display of *Coracias* species, already touched upon (see General Habits). Whether rolling displays function exclusively or mainly to advertise, to assert territorial rights, to maintain the pair-bond, or to intimidate a section of the population, or to what extent they are sexual, remains yet to be determined. With European Rollers, the best-known species, the rolling display is performed by males and not females, and is thought to serve mainly in the demarcation of territory; it is used in the week or so before egg-laying, mainly or exclusively when another male intrudes. The two males contest by rolling, and the sight of two birds simultaneously indulging in this behaviour has led some observers to claim that both sexes in a pair exhibit the rolling display. Observations of rolling by Purple and Racquet-tailed Rollers in Transvaal suggest that the behaviour is directed at neighbouring territory-owning pairs. Aside from rolling flights, several *Coracias* rollers also habitually fly at height above their territories, calling at short, regular intervals and sometimes half-rolling; again, the precise function of this is not understood. Only one other display has been described, the bowing display or "palaver" of European, Abyssinian and Indian Rollers, and this appears to be a greeting ceremony, used between members of a pair and sometimes when three or more birds, perhaps relatives, meet.

Little that can be interpreted as courtship behaviour has been described. Some mild posturing on the ground has been observed, and, in Africa, the presentation of a morsel of food by one European Roller to another is evidence of courtship feeding. It is such observations in Africa, and the paucity of them in Europe, that lead to the conclusion that, in this intercontinental migrant, pair formation takes place in the African winter quarters or on the way back to Europe. Courtship feeding of the female by the male and mutual preening are frequent at the nest, particularly in pairs whose eggs or young have died.

Very little is known about the breeding biology of most species of coraciid, at least in part because of the inaccessibility of their cavity nests, high up in trees, palms, cliff faces or the outsides of buildings. Nest-cavities are unlined, or there may be a few bents of vegetation, since it seems that rollers, like bee-eaters, occasion-

ally pick up a small dead leaf and fly with it to the nest, there to mandibulate and drop it. Some nest-holes have a small pad of vegetation. The eggs are laid about every second day, and clutches are generally of two to four eggs in the tropics and up to six at higher latitudes. All roller eggs are much alike, being white, smooth and glossy, only 1.20 to 1.25 times as long as they are broad, and of sizes varying little among the species, from 30.3 mm to 35.4 mm in length. Only the female incubates at night, but otherwise both parents appear to take more or less equal roles in raising the young.

Nestlings hatch at one-day intervals and so are staggered in size. At first they are naked and blind, unprepossessing pink creatures with a hugely swollen belly, fleshy legs, a thick yellow-white gape, a small white egg tooth and a prognathous jaw. Later, the skin becomes wrinkled, grey and shiny. At about two weeks of age, they are in what has been aptly described as the hedgehog stage, covered with long, grey spines, these being the as yet unopened feather sheaths. No down develops, and they leave the nest looking like short-tailed and dull-plumaged adults. For several species for which the fledging period is known, this is of the order of 25-30 days. Few people have succeeded in making detailed observations on a brood leaving the nest, and even in those cases where they have there remains the suspicion that the departure of some of the young birds may have been influenced by the presence of the observer. When the oldest chick appears ready to fly, its siblings still have a varying number of days of maturation left, yet the young probably seldom fledge in the orderly sequence in which they hatched. Instead, the whole brood seems to leave the nest over a period of a day or two, or even within a matter of hours. For a few days, the fledglings, scattered some metres apart from each other, remain heavily dependent upon their parents for food; almost nothing is known about the way in which they come to fend for themselves.

Making field studies of the Blue-bellied and Cinnamon Rollers in Ivory Coast, Thiollay discovered that, at least for those two species, the overall reproductivity of the population is low, owing to the fact that high proportions of adults do not breed at all in a particular year. In the group-living Blue-bellied Roller, males greatly outnumber females, and there was some evidence that both sexes



In rollers, the rate of food delivery to the nest apparently remains quite constant throughout the day, with a slight dip around midday and only short delays between feeds, especially when the brood is large and the nestlings mature. A captive juvenile roller was recorded consuming 40 medium-sized grasshoppers and 4-5 lizards in a day, so the adults, like the Purple Roller seen here, have to invest plenty of effort in raising their offspring, especially given that the brood may contain four hungry nestlings.

[*Coracias naevius mosambicus*, Zimbabwe. Photo: Eric & David Hosking/FLPA]





This Lilac-breasted Roller perches at the entrance to its nest with a large female earwig (Dermaptera) ready for presentation to its brood. Analysis of pellets apparently produced by nestlings and data from neck-collar experiments suggest that there is no significant difference between the diet of young and adult rollers, although presumably the items are smaller when chicks are young. Indeed, pellets are sometimes scarce inside nests before the tenth day after hatching, implying that the initial diet may consist of more delicate or perhaps partly digested food. Both adults supply approximately the same proportion of food to the nestlings, transporting items in their bills and delivering them whole into the nearest gape.

[*Coracias  
caudatus caudatus*,  
Kenya.  
Photo: M. Gore/FLPA]





Taking advantage of the handiwork of previous occupants, this Dollarbird has raised young in a termitarium, using a cavity excavated by Laughing Kookaburras (*Dacelo novaeguineae*). It carries a winged insect captured during one of its aerial forays. Dollarbirds, and other members of the genus *Eurystomus*, rarely take terrestrial prey. They are often crepuscular, and at such times can be seen swooping with great agility after flying prey. They often appear buoyant, sleek and rakish and are sometimes thus mistaken in failing light for large falcons or nightjars. The recipient of this food item is sufficiently mature to emerge from the cavity in anticipation of its meal, thereby reducing the adult's time at the nest. Its plumage is almost fully grown and the bird will shortly leave the nest, its yellow bill thereafter growing dusky and easily distinguishable from that of the adult.

[*Eurystomus orientalis pacificus*, south-east Queensland, Australia.  
Photos: Cyril Webster]

may be long-lived, with a lifespan quite likely to be well over twenty years; these are typical attributes of co-operatively breeding tropical birds. Those pairs that did breed in a given year produced an average of two fledglings, contributing to population increases during the breeding season of 14% in one year and 41% in another. Of 569 adult Cinnamon Rollers studied near Lamto in south Ivory Coast, 20% were thought to be unpaired. Of the pairs, about 15% evidently did not attempt to breed, and the clutches of a further 15% came to nothing; the remaining pairs, however, did well and, from their small clutches, elsewhere known to consist of two or three eggs, they produced an average of 1.4 flying young per pair.

## Movements

Little is known about the distances to which young rollers disperse. What is clear, however, is that most tropical coraciids are migratory and that the two temperate-latitude ones are highly so: the European Roller and the Dollarbird are intercontinental migrants which make movements that are spectacular. Azure Rollers, restricted to Halmahera, are not migratory, nor are island and some tropical mainland races of the Dollarbird. Blue-throated Rollers, living in the almost aseasonal African equatorial rainforest, and Racquet-tailed Rollers, confined to south-east African woodland, and even the widespread southern African race of the Lilac-breasted Roller, are mainly sedentary. In the northern tropics of Africa, Lilac-breasted, Abyssinian and Blue-bellied Rollers are partial migrants. In wet climates and green vegetation in the south of their ranges populations are resident, while in arid, subdesert steppe in the north each species is a breeding visitor that spends part of the non-breeding season among residents farther south. Lilac-breasted Rollers of the race *lori* are breeding summer visitors to north-west Somalia, and a few birds remain there all year, but after nesting the great majority departs in a mass migration, mov-

ing by day, to spend the off-season in south Somalia, there displacing some of the local population, which then migrate as far south as Tsavo East National Park for the non-breeding season.

Purple Rollers live across Africa, with northern and southern tropical subspecies separated by more than 1000 km. The northern population has movements similar to those of the Abyssinian Roller, being resident in Northern Guinean and Southern Soudanian zones in the latitudinal middle of its range, a dry-season or winter visitor to mesic Southern Guinean savanna woodland, and a wet-season or summer visitor north towards the Sahara in Northern Soudanian and Sahel zones. In the southern tropics the various populations move in much the same way, but with the timing shifted by six months. Ultimately determined by the annual oscillation of the African rains, which reach north nearly to the Sahara in July and south to Zimbabwe in January, a continent-wide pattern in the mirror-image movements of Purple Rollers north and south of the equator is readily discernible. Locally, however, the species' comings and goings sometimes seem not to accord with the pattern, and many details remain to be elucidated.

European Rollers winter exclusively in Africa, mainly in the east and south. Recoveries of ringed individuals show that some have round journeys of at least 20,000 km. In autumn many travel from east Europe to central Africa at an average speed of 67 km per day, and in spring back again at 110 km per day. Great numbers of birds are involved: L. H. Brown and B. E. Brown estimated that 2,000,000 spend the northern winter in Kenya, so several more millions must winter from Tanzania to Namibia and Transvaal. They usually fly by day, though some night migrants are trapped in Tsavo West National Park, mostly in November and December. In many places they fly evenly spaced on a broad front, one bird regularly following another at the same height and moving in the same direction, with dozens in view at once. In Chad, Sudan and Eritrea and, in the north-west Indian Subcontinent, from Punjab to Kachchh, this species is much commoner in autumn than in spring, and Wilson has proposed that, in autumn, Euro-



Here we witness a somewhat surprising occurrence, as this female European Roller delivers a small ball of mud "through the hatch" to her offspring.

The purpose of her supplying this material is far from clear, but one of the more convincing suggestions is that it may be ingested by the young birds in order to help them break down some of their less digestible food items, such as certain types of insect prey which are heavily chitinous. This nest is located in a hole that was originally excavated by a woodpecker, as is often the case with roller nests.

The European Roller is in regression throughout much of its range, mainly as a result of habitat loss, but also due to the use of pesticides, disturbance, and persecution. Within the context of habitat loss, one of the more precise problems in some areas appears to be a dearth of suitable nest-holes. In Extremadura, south-west Spain, the experimental provision of nest-boxes has proved encouragingly successful, with an increase in overall breeding success. It may be that this technique could be used to alleviate the situation elsewhere.

[*Coracias garrulus*,  
Nava del Rey,  
Valladolid, Spain.  
Photo: Javier Echevarri]







Nestling rollers usually hatch at one day intervals and are thus staggered in size throughout their development. On emergence they are pink, unsightly, blind and naked. The skin becomes wrinkled soon afterwards and the eyes open at 7-8 days old. At roughly the same age spine-like unopened feather sheaths emerge to create what has been termed the "hedgehog" stage, similar to that in related cavity nesters such as kingfishers (Alcedinidae) and bee-eaters (Meropidae). This adult European Roller stuffs an orthopteran into the gape of the hungriest nestling which tramples on its satiated, and somewhat less enthusiastic, siblings to reach the food item. The thick yellow-white gape can be seen, as can the remains of the small whitish egg-tooth on the tip of its bill.

[Coracias garrulus garrulus, Gard, France. Photo: Alain Christof/Oxford Scientific Films]

pean birds cross the Mediterranean and the Sahara in unbroken flight and that Asiatic ones enter Africa by way of the Red Sea. In spring, European Rollers start to congregate in east Tanzania in late March, and in early April there is a dramatic mass migration along the coastal lowlands of Kenya and Somalia, where tens or hundreds of thousands pass over one spot in a matter of hours, flying 300-500 m high, evenly spaced in an unending column several kilometres wide, and travelling at 48 km/h. Vast numbers also pass through Ethiopia in spring, but not through Sudan or Egypt. At that time, far more landfallen birds can be seen in all parts of the Arabian Peninsula than in autumn, but the innumerable thousands vacating Africa are lost to view and probably cross the Arabian desert in unbroken, high-altitude, day-and-night flight.

Few bird species have a greater latitudinal breeding range than the Dollarbird, which is a summer visitor to north China, the lower Amur and Manchuria from May to early September, and to New South Wales in Australia from October to early March. A few north-east Asian birds winter in Japan and south China, but most migrate south towards Malaysia. Some have been captured at night when crossing Fraser's Hill in Malaysia in October and November, but most seem to travel by day, in some places ones and twos passing high in the air every few seconds, like European Rollers in Tanzania, although spectacular mass movements of Dollarbirds have not been reported. Australian birds, after breeding, migrate north to New Guinea and Sulawesi, with a few remaining in north Australia. Adults leave first, followed a week or two later by the year's young. Forshaw speculates that there are two main routes into and out of north Australia, one across Torres Strait and the other across the Arafura and Timor Seas, the latter taken by birds that spend the off-season in the Lesser Sunda Islands and Sulawesi.

### Relationship with Man

It does seem surprising that such vividly plumaged and noisy birds, often living close to man in farmland and villages, should

have barely any discernible presence in human traditions or influences on mankind, yet, at least in Europe, that is the case. It is very likely that there are interesting myths, beliefs and rituals concerning rollers in those parts of the world with more coraciid species than Europe's singleton. If so, they have not found a place in the annals of ornithology, except that, in Kerala, Indian Rollers are supposed to be of medicinal value, and a broth made from their bodies is given as a cure for whooping cough.

The inspiration for these birds' names in several languages is the rolling flight display. This display, more accurately described in current English usage as "rocking", has been widely misinterpreted as somersaulting, or at least exaggerated as such in the repetitious recounting of it. No roller turns head over heels as used to be widely claimed, nor does any rotate its body through a whole 360°; rather, there is a rapid left-right-left twisting of the trunk and the flailing wings through about 180° or possibly 270°, with the head remaining level. Rolling flights are often directed at people, the bird practically parting the person's hair, but nothing more than a transient scare is occasioned.

Other common colloquialisms are "blue crow" or "blue jay", on account of the several crow-like attributes of some rollers. Furthermore, in Sri Lanka, the Indian Roller is colourfully known as "the one who inhales smoke", on account of its predilection for hunting around bush fires (see Food and Feeding), a habit which has also given that species the local name of "cousin to the fire".

Certain birds have featured disproportionately in renaissance European art, mainly because of their appealing form and unsurpassed colours. The European Goldfinch (*Carduelis carduelis*) is one example and the European Roller another. Albrecht Dürer's beautiful depiction of a detached wing of a Roller, painted in 1512, is a famous case in point. William Swainson described the artistic challenge in 1837. He wrote of the Cinnamon Roller that "The exquisite lilac reflections of the under plumage defy the painter's art", and of the Blue-bellied Roller that "No effort of art can possibly do justice to those inimitably rich lines of ultramarine, beryl colour, and changeable fawn, with which it is





The incubation period of the European Roller is 17-20 days and the provisioning period is 25-30 days. Thus, given the almost full feathering of the nestling pictured here gaping to receive a bush-cricket (*Tettigoniidae*), we can assume that eggs were laid in this cavity in France around six weeks previously and that the brood is about to fledge. Given the wide disparity in laying and hatching times, it is not surprising that fledging in rollers is asynchronous, sometimes spanning only a few hours, but occasionally up to 48 hours from first emergence to last. Parents have been noted calling for prolonged periods near the entrance hole, apparently tempting their progeny to vacate the confines of the nest. The first fledgling out is tended by one parent while the other continues to provide food for the more cautious and hesitant siblings keeping to the nest. This division of the brood between parents may continue after all the young have fledged. Young rollers tend to begin foraging independently around five days after fledging and are fully independent after three weeks or so. A loose family association is maintained for a further 3-5 weeks, after which the juveniles begin to wander from the territory one by one.

[*Coracias garrulus garrulus*, Gard, France. Photos: Alain Christof/Oxford Scientific Films]





ornamented; for there are no tints hitherto discovered, either mineral or vegetable, which will enable the painter to produce their successful imitation”.

### Status and Conservation

The latest assessment by BirdLife International lists one coraciid as globally threatened. This is the Azure Roller, known only from Halmahera and three small satellite islands. There have been few recent records of this species, and, with heavily increased pressure from logging and human settlement, the population has undergone a major decline in the last decade. As most of the forests on this island have now been given over to logging concessions, while the closely related Dollarbird is efficiently colonizing the cleared areas, the most urgent requirement is probably to establish a series of reserves, wherein the forest habitat would need to receive strict protection.

Of the other species, several could be said to be common, at least locally, but that is little reason for complacency, as indicated by the fact that populations of the best-studied species, the European Roller, have also shown an alarming decline in recent decades. Over much of its breeding range, the European Roller's density is of the order of 15 pairs per 100 km<sup>2</sup>, but in prime oak (*Quercus*) and pine (*Pinus*) woodland habitats concentrations of four, six and nine breeding pairs/km<sup>2</sup> have been recorded. On its wintering grounds, it was estimated that there were 500,000-700,000 in the Tsavo National Park and 2,000,000-3,000,000 in eastern Kenya, where this species outnumbers all of the native *Coracias* rollers by a factor of five to seven. The European Roller appears to be just as densely distributed in parts of Tanzania, Namibia and Botswana. Moreover, 500 migrants were once counted along 50 km of roadside wires in Atbara in Sudan, and 5000 at Dodoma in Tanzania, while at Balad, in Somalia, 40,000-50,000 migrants passed overhead on a single April day, a snapshot of the mass coastal migration there.

Formerly, however, that species must have been even more abundant, for in the last twenty or thirty years there has been a decline of breeding birds in Europe of almost catastrophic proportions. Rollers have disappeared from Sweden and Germany, and their numbers have fallen in a further 18 European countries. In Austria the breeding population decreased by over 90% between 1970 and 1990, and in Israel several thousand pairs nested in the 1950's but only 500-1000 thirty years later. Also in Israel, spring passage at Eilat has collapsed from hundreds or thousands of birds in the 1970's to no more than a few tens today.

A large proportion of the spring emigrants from Africa crosses the Red Sea and the Gulf of Aden, heading north-east for eastern Europe and west and central Asia. Those that make a landfall in Arabia are tired and perch conspicuously on the tops of bushes behind coastlines, where townships have grown greatly in recent years. In Oman, the birds are sitting targets for some young men equipped with powerful Japanese-manufactured air-guns, and large numbers are shot during the two weeks in May, just before the breeding season, when European Rollers are widely distributed and locally common to abundant. Along the Salalah Plain in south Oman, they are killed mainly in the three hours after dawn, in gardens and shrubby country; the heads are pulled off and the bodies taken away, presumably to be eaten. A hundred heads can be found in a matter of hours. The May harvest is evidently an ancient tradition, and in north Oman European Rollers continue to be shot extensively, near the coast and inland, around towns and in the country. Many spring migrants are killed also in the Farasan Archipelago, in the southern Red Sea.

Notwithstanding such slaughter, loss of habitat is almost certainly the main reason for the European Roller's decline. O. Samwald and F. Samwald have shown that, in Austria, intensive pesticide-dependent agriculture, with traditional meadows and pastures with scattered trees being transformed into treeless maize fields, has brought about the bird's collapse. In another region that those authors have studied, the Crau in south France, the species can be rehabilitated only by returning parts of the land, recently irrigated for maize crops and market gardening, back to its original steppe condition. The decline in abundance in Israel

In general, equatorial populations of rollers are sedentary, while those breeding in subtropical or temperate latitudes tend to migrate, often for great distances and in spectacular numbers. Spring flights of European Rollers (*Coracias garrulus*), for instance, passing northward through East Africa to their Palearctic breeding grounds, sometimes involve hundreds of thousands of flying birds in an apparently endless column several kilometres wide. All populations of this species migrate, whereas the Dollarbird (*Eurystomus orientalis*) is a partial migrant, with a see-saw migration pattern from the tropics into the Northern and Southern Hemispheres. While its tropical populations are largely resident, the bulk of its Australian population spends the non-breeding season (April-August) in New Guinea or Indonesia. Meanwhile, those breeding in China and Japan migrate in the opposite direction, reaching as far south as Malaysia (September-April). The nominate race of the Cinnamon Roller breeds only in Madagascar, crossing the Mozambique Channel to reach its African winter quarters, which apparently lie principally in Zaire. Although it breeds fairly commonly throughout Madagascar, it is here seen perched atop a plant (*Alluaudia*) endemic to the spiny forests of the south-west. Cinnamon Rollers return to this arid region in October and November, when their cackling territorial disputes and displays can be heard, especially as they squabble over potential nest cavities high in the ancient baobabs (*Adansonia*). Here, as elsewhere, they are particularly fond of flying termites that hatch after rain, and at dawn and dusk they congregate to feast aerobically alongside nightjars.

[*Eurystomus glaucurus glaucurus*, Berenty Reserve, south Madagascar. Photo: Kevin Schafer]



Fires, started naturally or anthropogenically, are attended, often in large numbers, by several roller species, including the Abyssinian Roller. The blazing inferno can be of considerable advantage to the rollers, as it causes potential prey to flee in desperation from cover, thus rendering it much easier to catch. This same situation is commonly exploited by other opportunists, including several species of raptor (Falconiformes) and other bird groups, such as drongos (*Dicruridae*) and some hornbills (*Bucerotidae*). In fact, deforestation generally tends to be beneficial to most rollers, as it typically produces open country, replacing closed habitat that is unsuitable for them.

[*Coracias abyssinicus*, Kenya.]

Photo: Don Smith/FLPA]



is attributable to habitat loss, disturbance and the use of pesticides. Sustained hunting pressure cannot help, especially since it occurs at a time immediately before the breeding season.

With animals in general, experience has taught that habitat loss usually has a far more rapid and profound effect on population sizes than do hunting or other adverse influences. Intensive slaughter may finish off a species, but hunting can often be practised indefinitely with no significant lasting effects, if the species has plenty of habitat in which to sustain and reproduce itself. For migratory birds to sustain themselves, it is essential that they have, in both the breeding and the non-breeding seasons, adequate reserves of habitats that are not too patchy.

Four species of roller, although presently widespread and common at least in large parts of their ranges, are at long-term risk through habitat destruction. They are all African, and all four inhabit woodland of types that are far easier for man to destroy than to regenerate. The Racquet-tailed Roller lives in the southern African miombo, mopane and *Baikiaea* biomes, the Lilac-breasted in *Acacia* savanna woodland, the Blue-bellied in the western African *Isoberlinia* woodland biome, and the Blue-throated Roller in west and central African lowland rainforest (see Habitat). If local, regional and complete-range census data are lacking for these rollers, there is plenty of sound information about the retraction and fragmentation of these woodland types during recent decades. In Nigeria, for example, there were over 50,000 km<sup>2</sup> of good lowland forest fifty years ago; today, although Blue-throated Rollers have survived in good numbers in the secondary forest that has sprung up where the primary stands have been felled, probably much less than 5000 km<sup>2</sup> of primary rainforest remains. All of these roller species will utilize a variety of woodland types, although it remains to be seen whether the Lilac-breasted and, in particular, the Racquet-tailed Rollers will flourish when much greater inroads into their preferred forest types have been made. Blue-bellied Rollers are no longer at all common in Nigeria, probably because the mesic woodland that formerly stretched from west to east across the middle of the country has largely disappeared, great swathes having been chain-felled for agricultural development. The Cinnamon Roller may also belong in this category, although its extensive range and greater use of humanized environments suggests that it is probably somewhat more secure.

At present, the Purple-winged Roller of Sulawesi seems to be locally quite common in the montane forest and lowland woods and farmland. However, it is poorly known, and requires further study.

The Dollarbird, as a species, is not under threat; it has a vast range and is generally common. Several of its subspecies are restricted to one or another tropical archipelago or island, and the most recent information suggests that their populations are for the most part reasonably healthy. In the Andaman Islands the race *gigas* is widely distributed and fairly common, in New Guinea *waigiouensis* is generally common throughout, and in the Solomons *solomonensis* remains not uncommon; on Simeulue *oberholseri* was widespread in the 1930's, but its current status is unknown. In Sri Lanka, the race *irisi* was always rare, with no records at all between 1890 and 1950, when a pair was found nesting and was shot; it was rediscovered in Sinharaja Forest in 1979, and a pair was seen nesting in 1980, since when there have been many sight records. The races of the Dollarbird are not very well differentiated, and field records in the tropics generally fail to distinguish between native populations and non-breeding visiting ones, so that abundances of some endemic races there may have been exaggerated. In the Philippines, the species was quite numerous in the 1950's and locally so up to the 1970's, but it is now uncommon, almost certainly as a result of the massive post-war deforestation that has taken place.

By contrast, the remaining three rollers, the Purple, Abyssinian and Indian, seem all to have benefited from changes in the countryside during the last few decades of the twentieth century. They are birds of light woodland where it abuts on to grassy, open country, and they are adaptable enough not only to find sustenance in pasture, cropland and green suburbs but also, in the case of the Abyssinian and Indian Rollers, to nest on buildings almost in preference to trees. Their future is probably assured, for as long as woodland clearance for intensive open-field agriculture fails to dominate over traditional, tree-retaining land use.

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# Genus *CORACIAS* Linnaeus, 1758

## 1. Purple Roller

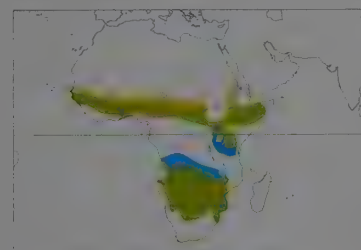
### *Coracias naevius*

**French:** Rollier varié **German:** Strichelracke **Spanish:** Carraca Coroniparda  
**Other common names:** Rufous-crowned Roller

**Taxonomy.** *Coracias naevia* Daudin, 1800, Senegal. Relationships uncertain; no obvious close allies. Species name frequently given as feminine, *naevia*, as in original description, but genus is masculine. Original spelling of species name actually appears to be "noevia", but appearance of diphthongs varies with original typescripts, and evidence from this same work indicates author's intended name to have been "naevia". Two subspecies recognized.

#### Subspecies and Distribution.

*C. n. naevius* Daudin, 1800 - Senegal E to Somalia, and S to Tanzania.  
*C. n. mosambicus* Dresser, 1890 - Angola and Namibia E to Zambia, S Mozambique and NE South Africa (N Natal).



**Descriptive notes.** 35-40 cm; 125-200 g. The heaviest African roller. Nominative race with pinkish-rufous crown and nape, striking white supercilia, olive-green back; entire underparts white-streaked pink. Differs from other African *Coracias* species in pattern of underparts and lack of any pale azure-blue in plumage; from African *Eurystomus* rollers in long black bill and olive (not tan) back. Sexes alike. Immature pale olive on head and underparts. Race *mosambicus* larger, crown and hindneck olive, ground colour of underparts more purple.

**Habitat.** Open savanna woodland and farmland with spaced large trees, also rocky and shrubby

hillsides and arid *Acacia* savanna; in hot lowlands mainly below 1300 m; sometimes up to 3000 m.

**Food and Feeding.** Large insects and small vertebrates: locusts, grasshoppers, mantises, beetles, ants, scorpions, lizards, snakes, rodents, young birds. Hunts from perch mainly high in trees, but also uses telegraph wires. Prey taken mainly from surface of ground.

**Breeding.** Mar-Sept in N tropics, Feb-Nov in E Africa, Sept-Dec in S tropics (mainly Sept-Oct in Zimbabwe), but May-Jun in Namibia. Monogamous; conspicuously territorial, with dashing and rocking or tumbling aerial display ending in fast glide; also has fast, more horizontal rolling flight. Nest placed in cavity high in tree, in tall sand cliff by streambed, in rock cliff or masonry, probably sometimes in high termite mound. Clutch of 2-4 eggs; incubation period, appearance of chicks and other details unknown.

**Movements.** In N tropics found all year in N Guinean and S Soudanian savanna, but a dry-season (Nov-Feb) visitor to S Guinean woodland and a wet-season (May-Sept) one to Sahelian zone; rare dry-season visitor to Liberia, with 14 records since 1980's, but only vagrant in Sierra Leone; in E Africa nomadic, with tendency to move S in non-breeding period or if a drought in N. In S tropics the converse of the N: resident in Zimbabwe but commoner in May-Dec, and with post-breeding dispersal into dry country in S and SW, and in S Mozambique in Jun-Sept; in Zambia mainly non-breeding visitor May-Oct, sometimes from Mar. Recorded as vagrant in Yemen.

**Status and Conservation.** Not globally threatened. Widespread N and S of equatorial forest zone, and widespread in E Africa; rather sparse, although highly visible, over much of range, but locally frequent or even abundant, e.g. once 1 every 200 m on roadsides on Acacia Plains, in Ghana, and once c. 5/km<sup>2</sup> in Tsavo National Park, Kenya; density of S tropical population about same as that in N. Few firm data, but species possibly not adversely affected by timber clearance for farmland creation, provided that spaced large shade trees are preserved, and it may even benefit through easier foraging where ground cover is cleared. In Zambia, however, few recent records NE of R Lunsemfwa, where species was formerly frequent. Occurs in a number of protected areas, e.g. Benoue National Park (Cameroon) and Daan Viljoen Reserve (Namibia).

**Bibliography.** Anon. (1998b), Archer & Godman (1937-1961), Ash & Miskell (1998), Balança & de Visscher (1996), Bannerman (1933, 1953), Barlow *et al.* (1997), Benson & Benson (1977), Benson *et al.* (1971), Britton (1980), Brown & Britton (1980), Brown & Brown (1973), Cave & Macdonald (1955), Cheesman & Selater (1935), Cheke & Walsh (1996), Clancey (1996), Dean (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgood, Fry & Dowsett (1973), Elgood, Heigham *et al.* (1994), Friedmann (1930a), Fry *et al.* (1988), Gatter (1997), Ginn *et al.* (1989), Giraudoux *et al.* (1988), Gore (1990), Grimes (1987), Harrison *et al.* (1997), Herremans & Herremans-Tonnoeyr (1994b), Lamarque (1980), Lewis & Pomeroy (1989), Lippens & Wille (1976), Louette (1981b), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Morel & Morel (1990), Mullie *et al.* (1991), Penry (1994), Pinto (1983), Short *et al.* (1990), Snow (1978), Steyn (1996b), Thiollay (1971a, 1973b, 1985a, 1985b), Urban & Brown (1971), Zimmerman *et al.* (1996).

## 2. Indian Roller

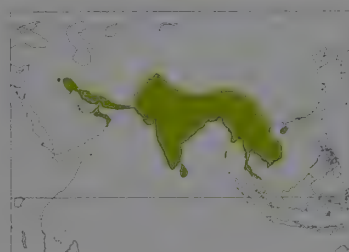
### *Coracias benghalensis*

**French:** Rollier indien **German:** Hinduracke **Spanish:** Carraca India  
**Other common names:** Blue Jay(?)

**Taxonomy.** *Corvus benghalensis* Linnaeus, 1758, Bengal (= Madras). Most closely allied congener is perhaps *C. caudatus*. May be closely related to *C. temminckii*. Race *affinis* sometimes given full species status, but intergrades with nominate race. Three subspecies recognized.

#### Subspecies and Distribution.

*C. b. benghalensis* (Linnaeus, 1758) - E Iraq and SE Arabia through N Pakistan and E to Bangladesh, S to Maharashtra.  
*C. b. indicus* Linnaeus, 1766 - C India (from S Maharashtra and Andhra Pradesh) S to Sri Lanka.  
*C. b. affinis* McClelland, 1840 - NE India (Bihar, Assam) E to SC China (S Sichuan, Hainan, Yunnan), and S to peninsular Thailand and Indochina.



**Descriptive notes.** 30-34 cm; 166-176 g. The only roller with an azure stripe across distal half of primaries, visible in flight from afar; tail rather short. Nominative race has blue crown, brownish back; cheeks and breast lilac with whitish streaks, belly pale blue; bill blackish, with dull orange base to lower mandible; orbital skin yellow. Differs from *C. garrulus* in lilac breast and (in flight silhouette) shorter neck; from *Eurystomus orientalis* in black (not red) bill and in broad stripe (not azure patch) on primaries. Sexes alike. Immature differs in most colour shades and is overall duller. Race *indicus* brighter than nominate *benghalensis*; *affinis* much darker, with purple breast and dark olive back, hardly streaked on throat.

**Habitat.** Open farmland, pasture, stubble, plantations, palm groves, dry *Acacia* and *Prosopis* woods, roadsides with telegraph wires and wayside grass; also villages, preferably with a few tall buildings, and old and modern buildings near shrubby or green places in suburbs and cities; also parks, playing fields, large gardens, and grassy roundabouts.

**Food and Feeding.** Large arthropods and small vertebrates: grasshoppers, crickets, earwigs, mantises, bugs, termites, beetles, moths, wasps, ants, larvae, scorpions, spiders, lizards, snakes, frogs, toads, mice, shrews, occasional fish and young birds. Most food taken on ground. Forages all day, even in shade temperatures over 40°C; continues to feed well into dusk, and even at night. Watches from elevated, exposed perch, e.g. edge of roof, side of small tree, wire, lamppost, farm shed or machinery, or hay stook; on sighting prey, descends in leisurely-looking glide, alights next to prey and snatches it in bill; then beats it against ground, or moves to a hard perch to do so; most vertebrates swallowed whole. Sometimes hovers momentarily above prey. Insects, including cicadas, taken on the wing after brief flight; sometimes takes insects attracted to street lights. Dives into water for frogs, and may briefly submerge. Scavenges roadkills. Strongly attracted to grass and bush fires, pursuing prey through smoke.

**Breeding.** Mar-Jun (rarely Jul) in N, Jan-Mar in S. Monogamous; conspicuously territorial, patrols territory in high, semi-rolling flight, calling. Lays in simple nest in masonry cavity, under eaves, in roof overflow pipe, in tree hole, or hollow at top of dead coconut palm, or hole in clay or sand cliff; bits of grass, paper and rag brought by both sexes to line cavity. Clutch of 3-5 eggs; replacement sometimes laid; incubation, mainly by female, 17-19 days; fledging 30-35 days. At 9 nests in India, 36 eggs produced 24 young.

**Movements.** Breeds in SE Arabia, but also regular and abundant winter visitor there; since species is not known as a migrant in Pakistan, Oman birds may come from India. Elsewhere, less obviously migratory, but subject to ill-understood local movements; for instance, in S Myanmar common only in Sep-May, but no evidence of migration farther S. Recorded as vagrant in Syria.

**Status and Conservation.** Not globally threatened. Common over much of its range; locally abundant, at least seasonally in many areas; very common and conspicuous in SE Asia. In Oman, once 370 birds on 250 km of roadside wires, and up to 200 on one new-cut 50 ha fodder field. Likely to have increased with deforestation and urbanization; breeding population in N Oman and United Arab Emirates probably now in thousands. Has expanded range in Iraq, N to Baghdad. Not known to be hunted regularly, but, being roadside scavengers, many are struck down by vehicles. Species is killed in Kerala for its supposed medicinal value. Occurs in many national parks, e.g. Golestan (Iran), Khirithar (Pakistan), Chitwan (Nepal), Bharatpur, Kaziranga and Periyar (India), Uda Walawe and Yala (Sri Lanka), Khao Yai (Thailand) and Nam Bai Cat Tien (Vietnam).

**Bibliography.** Ali (1996), Ali & Ripley (1983), Ali *et al.* (1996), Amstutz (1973), Aspinall (1994, 1996), Beaman & Madge (1998), Bharos (1990, 1992), Biddulph (1937), Biswas (1961a), Chimoy (1971), Coles (1996), Cramp (1985), Dalgleish (1911), Deignan (1945), Duckworth *et al.* (1999), Eriksen & Eriksen (1999), Étiéhcopar & Hue (1978), Evans, G.H. (1921), Evans, M.I. (1994), Gallagher & Woodcock (1980), Goenka (1986), Grimmett *et al.* (1998), Harrison (1999), Harvey (1990), Henry (1998), Hollom *et al.* (1988), Hue & Étiéhcopar (1970), Jennings (1981b, 1995), Jeyarajasingam & Pearson (1999), Lamba (1963), Lekagul & Round (1991), McClure (1998), Medway & Wells (1976), Meyer de Schauensee (1984), Mukherjee (1995), Phillips (1978), Porter *et al.* (1996), Radcliffe (1910), Ravi (1966), Richardson (1990, 1994), Ripley (1982), Roberts (1991), Robson (2000a), Rutgers & Norris (1977), Sharga (1936), Smythies (1986), Snow (1978), Snow & Perrins (1980), Stepanyan (1995), Stonor (1944), Sugathan & Varghese (1996), Tiwary (1930), Wells (1999), Yang Lan *et al.* (1995), Zhang Ciu *et al.* (1997), Zhao Zhengjie (1995).

## 3. Purple-winged Roller

### *Coracias temminckii*

**French:** Rollier de Temminck **German:** Celebesracke **Spanish:** Carraca de Célebes  
**Other common names:** Sulawesi/Celebes/Temminck's Roller

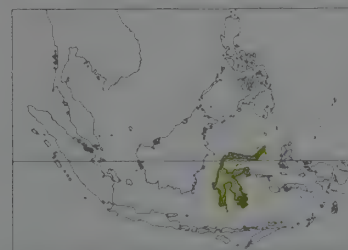
**Taxonomy.** *Garrulus Temminckii* Vieillot, 1819, India; error = Sulawesi.

Relationships uncertain. Closest relative probably *C. benghalensis* of race *affinis*. Monotypic.

**Distribution.** Sulawesi and offshore islands of Manterawu, Bangka, Lembeh, Muna and Butung.

**Descriptive notes.** 30-40 cm; 144-164 g. Unmistakable, the only breeding roller in Sulawesi. Plumage predominantly deep purple, with pale azure crown and uppertail-coverts, olive back. Saturated, unmarked wings and tail recall African *C. naevius*, but differs in azure crown and uppertail-coverts and unstreaked underparts; distinguished from *Eurystomus orientalis* and *E. azureus* by black bill, azure crown and uppertail-coverts, olive back, and solid purple wing lacking azure patch. Sexes alike. Immature has duller crown, olivaceous wing-coverts, and sooty-brown underparts with purple wash only on belly.

**Habitat.** Lives in partially closed, heavily wooded areas outside primary forest, at up to 1000-1150 m, including forest edge, large clearings with plentiful big trees remaining, alive or dead; sometimes on treetops in primary forest. At altitudes below 800 m and down to sea-level, inhabits light woodland, swamp forest, wooded savanna, open scrub woodland, cultivation, and edges of villages with gardens and smallholdings, where makes free use of telegraph wires and dead branches of tall trees.



**Food and Feeding.** Diet includes locusts, grasshoppers, beetles and small lizards. Sits on prominent perch, whence drops to ground to snatch prey; also seen snatching insects from outer foliage of trees.

**Breeding.** Eggs found in Nov: well-grown young in nests in late Sept, early Dec; young being fed in Mar. Few nests found to date, all in tree holes 5–20 m above ground, one a knothole, another an old woodpecker hole, one 10 m up a dead palm trunk. Clutch of 3 eggs. No further information.

**Movements.** Resident and sedentary, so far as known.

**Status and Conservation.** Not globally threatened. In parts of Sulawesi, said to be rather common or locally common; no estimates of density or abundance have been made, but average home range appears to occupy many hectares. How this species responds to man-induced habitat change is not known. Occurs in Dumoga-Bone and Lore Lindu National Parks.

**Bibliography.** Andrew (1992), Andrew & Holmes (1990), Baltzer (1990), van Bommel & Voous (1951), Catterall (1997), Coates & Bishop (1997), Ekstrom *et al.* (1998), Fraser & Henson (1996), Gibbs, D. (1990), Gregory-Smith (1998), Holmes, D.A. & Philipps (1996), Holmes, P. & Wood (1980), Inskipp *et al.* (1996), Rozendaal & Dekker (1989), Snow (1978), Stresemann (1940), Wardill (1995), Watling (1983), White & Bruce (1986).

## 4. Racquet-tailed Roller

### *Coracias spatulatus*

French: Rollier à raquettes

German: Spatelracke

Spanish: Carraca de Raquetas

Other common names: Weigall's Roller (*weigalli*)

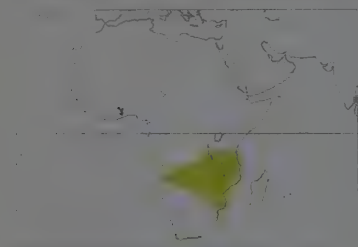
**Taxonomy.** *Coracias spatulatus* Trimen, 1880, Victoria Falls, Zimbabwe.

Affinities uncertain; possibly closer to *C. abyssinicus* than to *C. caudatus*. Status of race *weigalli* disputed; has been thought to be merely half-moulded immature of present species, but other authors regard it as a valid, geographically distinct taxon; the two races evidently hybridize over c. 200-km-wide area from S Tanzania through Malawi to C Mozambique. Species name frequently given as feminine, *spatulata*, but genus is masculine. Two subspecies currently recognized.

**Subspecies and Distribution.**

*C. s. spatulatus* Trimen, 1880 - W Angola E to W Tanzania and Mozambique (S of R Zambezi).

*C. s. weigalli* Dresser, 1890 - S Tanzania and N Mozambique (N of R Zambezi).



**Descriptive notes.** 28–30 cm (with streamers up to 8 cm more); 88–111 g. The smallest, lightest *Coracias*, with long tail and streamered outer rectrix with spoon-like tip. Nominative race with white forehead and supercilia, dull greenish-olive crown and nape, rufous-brown back and greater coverts, dark blue rump; wings dark blue, with azure bases to most remiges forming wingstripe; tail dark blue, outer feathers mostly azure, outermost elongated into blackish streamer 2–3 mm wide with spatulate tip; cheeks and entire underparts pale blue. Sexes alike. Immature typically lacks tail-streamers and white in eyebrow, has pale buffy-pink cheeks

and breast with broad whitish streaks. Race *weigalli*, with white-streaked pink on cheeks, throat and breast, resembles adult and, even more so, immature *C. caudatus* of nominate race; hybrids between *weigalli* and nominate *spatulatus* vary, perhaps clinally, in amount of white-streaked pink.

**Habitat.** Undisturbed, mature *Brachystegia*, *Colophospermum* and *Baikiaea* woodland and well-wooded *Acacia* savanna, up to 1300 m. Occupies more densely wooded areas than African congeners.

**Food and Feeding.** Locusts, grasshoppers, beetles, maggots, scorpions and small lizards. Forages by perching on mid-storey lookout, swooping down to take prey on ground.

**Breeding.** Lays in Sept–Dec. Nest is an unlined cavity, often an old woodpecker or barbet hole, 6–7 m up in tree. Clutch of 2–4 eggs. No other information.

**Movements.** Appears to be essentially sedentary, but locally nomadic; occurrence of *weigalli*-like hybrids in Zambia and Zimbabwe, W to Victoria Falls, may involve non-breeding migrants from NE.

**Status and Conservation.** Not globally threatened. Widespread and fairly common in Zambia and Zimbabwe; widespread but uncommon in Tanzania, N to Busondo and Kikore; uncommon to frequent but local in Malawi; scarce in NE Namibia, NE Botswana, Swaziland and Ndumu, in South Africa. Its evident dependence on undisturbed miombo and mopane woodlands, which are contracting owing to human pressures on them, means that, in the long term, the species is unlikely to do well. Occurs in a number of national parks, e.g. Mikumi and Ruaha (Tanzania), Kafue and South Luangwa (Zambia), Liwonde (Malawi) and Hwange (Zimbabwe).

**Bibliography.** Benson & Benson (1977), Benson *et al.* (1971), Britton (1980), Brooke (1984), Cattermole (1992), Clancy (1969, 1996), Coles (1996), Dean (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Ginn *et al.* (1989), Harrison *et al.* (1997), Howells (1970), Leonard (1998b), Lippens & Wille (1976), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Newman (1996), Parker (1999), Penry (1994), Pinto (1983), Randall (1993, 1996), Robertson (1998), Short *et al.* (1990), Sinclair, I. *et al.* (1993), Sinclair, J.C. (1987), Sinclair, J.C. & Whyte (1991), Snow (1978, 1979), Steyn (1996b).

## 5. Lilac-breasted Roller

### *Coracias caudatus*

French: Rollier à longs brins

German: Gabelracke

Spanish: Carraca Lila

Other common names: Lilac-throated Roller (*lori*)

**Taxonomy.** *Coracias caudata* Linnaeus, 1766, Angola.

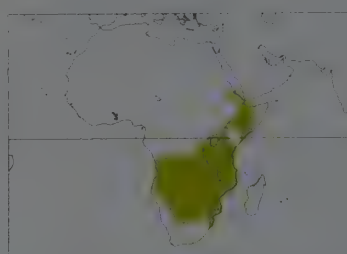
Often regarded as forming a superspecies with *C. abyssinicus* and *C. garrulus*, though probably more closely allied to former. Species name frequently given as feminine, *caudata*, as in original description, but genus is masculine. Two subspecies recognized.

**Subspecies and Distribution.**

*C. c. lori* Shelley, 1885 - Eritrea S to Somalia and NE Kenya.

*C. c. caudatus* Linnaeus, 1766 - Angola E to C & E Kenya, S to Namibia and N South Africa.

**Descriptive notes.** 28–30 cm (with streamers up to 8 cm more); 87–135 g. A lightweight roller, with streamered tail. Nominative race with whitish forehead and supercilia, glossy olive-green crown and hindneck, warm brown back, dark blue rump, azure uppertail-coverts; wings dark blue, including lesser coverts, rest of wing-coverts paler blue, primary coverts and bases of remiges brilliant azure-blue; tail bluish-olive, outer feathers azure-blue with dark tips, outermost elongated into black streamer; cheeks orange-pink, lower throat and breast lilac with white streaks, belly blue. Differs from *C. abyssinicus* in greener crown, orange-tinged cheeks, and pink throat. Sexes alike. Immature duller, lacks tail-streamers, has forehead and eyebrow buffish, and has buffish cheeks and



breast with broad whitish streaks; very like immature *C. spatulatus*, especially of race *weigalli*, but with pale blue-grey (not rufous-brown) greater coverts. Race *lori* has the breast blue, not lilac.

**Habitat.** *Acacia* woodland with well-spaced trees, pure grassland (where it uses any elevated perch, e.g. fence or telegraph wire), rolling bushy gamelands, light forest, riverside woods, and cultivated land. Does not associate with human habitation.

**Food and Feeding.** Arthropods and small vertebrates: locusts, grasshoppers (including the noxious *Phymateus viridipes*), crickets, beetles, butterflies, moths, hairy caterpillars, ants, scorpions, centipedes, spiders, snails, frogs, lizards

and birds. Keeps station on an elevated perch; swoops down to land next to prey on ground, seizes it in bill, and swallows it whole or dismembers it. Attracted to bush fires to forage on fleeing insects.

**Breeding.** Lays Apr–Jun (once Sept) in Somalia, Mar–Nov in E Africa, Aug–Nov in Zambia, and Aug–Dec in Zimbabwe and South Africa. Strongly territorial, pugnacious and vocal in defence of territory. Nest a flat pad of a few bits of grass, in a cavity 5 m up in dead tree or palm. Clutch of 2–4 eggs; incubation by both sexes, period 22–24 days; nestling covered in grey down at 5 days, fully feathered at 19 days; in captivity, fledging period 35 days, young fed by parents for c. 10 days further.

**Movements.** Nominative race is resident, with some dispersal in Zanzibar, Zambia and Zimbabwe. Race *lori*, after breeding in NW Somalia, migrates in Sept to winter in S Somalia; population breeding in S Somalia and NE Kenya moves to C & S Kenya, spending non-breeding season there, Dec–Mar. Recorded as vagrant in Yemen.

**Status and Conservation.** Not globally threatened. Abundant in Somalia; common in E Africa and Malawi and in parts of Ethiopia and Zambia; frequent in Zimbabwe except E; frequent in Transvaal S to around Swaziland border. Density in E Kenya estimated at 4 birds/km<sup>2</sup>. Occurs in many national parks, e.g. Awash (Ethiopia), Lake Mburo (Uganda), Nairobi, Tsavo East and Tsavo West (Kenya), Ruvuvu (Burundi), Liwonde (Malawi), Chobe (Botswana) and Etosha (Namibia).

**Bibliography.** Anon. (1995a, 1998b), Archer & Godman (1937–1961), Ash & Miskell (1998), Aspinwall (1984b), Barry (1998), Benson & Benson (1977), Benson *et al.* (1971), Bowen (1979), Britton (1980), Brown & Britton (1980), Brown & Brown (1973), Cockburn (1989), Coles (1996), Collard & Collard (1969), Dean (2000), Demy *et al.* (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Friedmann (1930a), Fry *et al.* (1988), Ginn *et al.* (1989), Harrison *et al.* (1997), Herremans & Herremans-Tonnoeyr (1994b), Irwin & Steyn (1977), Lewis & Pomeroy (1989), Lippens & Wille (1976), Macdonald (1940), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Pakenham (1979), Parker (1999), Penry (1994), Pinto (1983), Rutgers & Norris (1977), Shaw (1979), Short *et al.* (1990), Simmons (1979b), Snow (1978), van Someren, V.D. (1947), van Someren, V.G.L. (1956), Soroczynski (1994a, 1994b), Stander (1958), Steyn (1996b), Urban & Brown (1971), Vanderplank (1942), Zimmerman *et al.* (1996).

## 6. Abyssinian Roller

### *Coracias abyssinicus*

French: Rollier d'Abyssinie

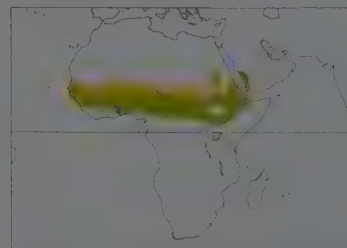
German: Senegalracke

Spanish: Carraca Abisinia

**Taxonomy.** *Coracias abyssinica* Hermann, 1783, Ethiopia.

Often regarded as forming a superspecies with *C. caudatus* and *C. garrulus*, though probably more closely allied to former. May be closely related to *C. spatulatus*. Species name frequently given as feminine, *abyssinica*, as in original description, but genus is masculine. Monotypic.

**Distribution.** Senegal to E Ethiopia, N to Sahara, and S to edge of rainforest zone; occasionally into desert, N to coastal NW Mauritania (Nouadhibou) and NC Sudan (Khartoum); also SW Arabia (has nested at least in S Yemen).



**Descriptive notes.** 28–31 cm (with streamers up to 12 cm more); 99–140 g. Head pale blue with white forehead and chin; upperparts brown, with rump, tail-coverts and centre of tail dark blue; tail mostly bright azure-blue, outermost feather greatly elongated into thin black streamer; wings dark blue, including lesser coverts, rest of wing-coverts bright pale azure-blue; entire underparts pale blue, throat to upper breast thinly streaked white. Differs from *C. caudatus* in longer tail-streamers, blue throat; from *C. garrulus* in slighter and more agile appearance, shorter neck (in flight silhouette), shorter wings, longer tail, and in purple-blue (not mostly black) remiges. Sexes alike. Immature lacks streamers, is duller than adult, with blue parts tinged olive.

**Habitat.** Dry woodland with well-spaced trees, pasture, tilled ground, cereal and cassava fields, thorny savanna, areas around marshes, clearings in woods, roadsides, and burnt shrubland; also rural housing estates, villages, and town parks and suburbs with plenty of vegetation and open space.

**Food and Feeding.** Eats larger insects: crickets, grasshoppers, beetles and caterpillars. Forages by watching ground from perch on tree, rooftop or telegraph wire; flies down, glides last few metres, alights by prey, sometimes hops clumsily after it, seizes it in bill, and gulps it down whole, or may fly to elevated perch to dismember it. Catches a few insects on the wing. Gathers in flocks of c. 20 at bush fires or antelope herds to exploit insects that are put up.

**Breeding.** Lays in Feb–Jul, later in Ethiopia. Monogamous; territorial, advertises territory with aerial display, suddenly plunging down on closed wings, levelling out and flying fast, shrieking and rolling rapidly, sweeping up again and repeating sequence; flies down at human intruder, veering away at last instant. Eggs laid on a few bits of vegetation in small hole in tree, palm trunk, termite hill or, commonly, in inhabited building, under eaves or in brickwork cavity. Clutch of 3–6 eggs; no information on incubation and fledging periods.

**Movements.** Mainly resident in Sudanian savanna zone; a breeding wet-season visitor to Sahelian zone N of c. 15° N, and a mainly non-breeding dry-season visitor to Guinean woodland farther S. Pronounced passage in Gambia in Jan–Mar and Jul–Aug, and on E shore of L. Albert, in Uganda, in Oct–Nov. SW Arabian population thought to be mainly resident. Recorded as vagrant in Libya, Egypt, Somalia and Angola.



**Status and Conservation.** Not globally threatened. Widespread, and frequent to common throughout range; locally abundant. Occurs in several national parks, e.g. Djoudj (Senegal), Comoe (Ivory Coast), Waza (Cameroon), Dinder (Sudan), Awash (Ethiopia) and Kabalega Falls (Uganda). Likely to have benefited from the spread of modern agriculture and small-town urbanization. Not known to be persecuted.

**Bibliography.** Balança & de Visser (1996), Bannerman (1953), Barlow *et al.* (1997), Bates (1927), Beaman & Madge (1998), Britton (1980), Brooks *et al.* (1987), Brown & Britton (1980), Cave & Macdonald (1955), Cheesman & Selater (1935), Cheke & Walsh (1996), Colston & Curry-Lindahl (1986), Cramp (1985), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgood, Fry & Dowsett (1973), Elgood, Heigham *et al.* (1994), Échécoar & Hue (1964), Evans, M.I. (1994), Field (1999), Friedmann (1930a), Fry *et al.* (1988), Giraudoux *et al.* (1988), Goodman *et al.* (1989), Gore (1990), Grimes (1987), Hazevoet (1996b), Hollom *et al.* (1988), Jennings (1995), Lamarche (1980), Lewis & Pomeroy (1989), Lippens & Wille (1976), Louette (1981b), Mackworth-Praed & Grant (1957, 1970), Morel & Morel (1990), Moynihan (1988), Mullié *et al.* (1991), Parker (1966), Plütke & Halley (1995), Porter *et al.* (1996), Rands *et al.* (1987), Rutgers & Norris (1977), Short *et al.* (1990), Smalley (1983), Snow (1978), Snow & Perrins (1998), Thonnerieux (1988), Tye & Tye (1983), Urban & Brown (1971), Zimmerman *et al.* (1996).

## 7. European Roller

### *Coracias garrulus*

**French:** Rollier d'Europe      **German:** Blauracke      **Spanish:** Carraca Europea  
**Other common names:** Eurasian/Blue/Common Roller

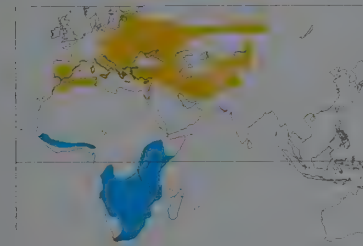
**Taxonomy.** *Coracias Garrulus* Linnaeus, 1758, Sweden.

Often regarded as forming a superspecies with *C. caudatus* and *C. abyssinicus*, though those two are probably more closely allied to each other than either is to present species. Two subspecies recognized.

**Subspecies and Distribution.**

*C. g. garrulus* Linnaeus, 1758 - NW Africa, SW, SC & E Europe and Asia Minor E through NW Iran to SW Siberia.

*C. g. semenowi* Loudon & Tschusi, 1902 - Iraq and Iran (except NW) E to Kashmir, N to Turkmeniya, S Kazakhstan and NW China (W Sinkiang).



**Descriptive notes.** 31-32 cm; male 127-160 g, female 130-154 g; birds wintering in Africa c. 120 g. A large roller without tail-streamers, proportionately larger-headed than most congeners, and in flight appears long-necked. Nominant race with head, neck and underparts light blue; whitish around base of bill, and short, thin blackish eyestripe; rufous-brown upperparts, with back, rump and tail-coverts ultramarine-blue; wing-coverts greenish-blue, marginal ones purple, primary coverts and bases of primaries azure-blue; remiges otherwise black, with purple only on inner secondaries, and undersides bright violet-blue; tail

greenish-blue with darker base, central feathers greyish, outermost tipped black and slightly longer than rest. Most similar in plumage to *C. abyssinicus*, differs in lack of streamers, and much stockier build. Sexes alike. Immature duller, head and tail olivaceous-green, breast and lesser wing-coverts tinged rufous, cheeks and chin to breast narrowly streaked with white; tail lacks black corners. Race *semenowi* slightly paler than nominate.

**Habitat.** Warm, sunny lowlands, at up to 1000 m in Europe and 2000 m in Morocco, in open countryside with patches of oak (*Quercus*) forest, mature pine (*Pinus*) woods with heathery clearings, orchards, mixed farmland, broad river valleys, and dissected plains with scattered thorny or leafy trees. On African wintering grounds, inhabits dry wooded savanna and bushy plains, in Tanzania also sisal fields and clearings in montane forest, and in W Africa cultivation in derived savanna woodland; also edges of secondary forest; below 1500 m.

**Food and Feeding.** Invertebrates, mainly beetles and other hard-bodied insects, and some small vertebrates: beetles of at least 14 families represented in diet, including longicorns (Cerambycidae), chafers and scarabs (Scarabaeidae), and click beetles (Elateridae); also crickets, bush-crickets, mole-crickets (Gryllotalpidae), locusts, grasshoppers, mantises, cicadas, Hymenoptera, termites, butterflies, caterpillars and flies; scorpions, centipedes, millipedes, spiders, molluscs, earthworms, frogs, slow-worms (*Anguis*), lizards, snakes, voles, shrews and exhausted small birds together comprise c. 3% of prey items. Exceptionally, fruits such as grapes and figs eaten. Most insect prey 10-30 mm long. Many live scorpions taken, and species may be an accomplished scorpion predator; several other prey items are distasteful, e.g. stink-grasshoppers (*Zonoceros elegans*) and carabid, lampyrid and silphid beetles. Forages mostly from elevated perch, watching ground intently; other recorded techniques include fly-catching from perch, following plough on farmland, and even sustained aerial hunting like a swallow (Hirundinidae). In Africa, will attend hatches of termites or ants, snatching the alates from the air one at a time.

**Breeding.** Lays in May-Jul. Monogamous; normally solitary and territorial, with typical rolling and diving aerial display, rarely semi-colonial with inter-nest distances of 70-200 m, exceptionally even 5-10 m. Nest-site an unlined cavity in a large tree, building, cliff or riverbank. Clutch of 3-6 eggs, usually 4-5; single-brooded, though replacement clutch will be laid; incubation, mainly by female, 17-19 days; chick hatches naked and blind, has closed spiny feather sheaths by 13th day, sheaths open from 17th day; fledging period 25-30 days, mostly 26-27; young fed by adults for further 3 weeks or more.

**Movements.** An intercontinental migrant, almost entire world population wintering in Africa S of Sahara. In autumn has occurred in great abundance in Algeria and Morocco, though only small numbers winter in W Africa; strong passage up Nile Valley and on W coast of Red Sea, also across Ethiopia, and in Oct-Dec through E Africa, especially Rift Valley; weak passage through Arabia. Winters mainly in E & SW Africa in Kenya, Tanzania, NE Botswana and E Namibia; present in Oct-Apr/May in S Africa, where prone to flock, evidently still moving S in Nov-Dec, and seen in SW Cape Province only in Dec-Feb. Congregates in E Tanzania from late Mar, and in early Apr up to hundreds of thousands travel N in narrow corridor along E coastal lowlands to NE Somalia, in one of continent's most spectacularly visible migrations, with thousands passing over a given locality in a few hours, e.g. 40,000-50,000 at Balad, Somalia, on single day in Apr; in Somalia, migrants fly 300-500 m above land, evenly spaced in column several km wide, at ground-speed of c. 48 km/h; also common to abundant in Ethiopia in Apr. From Somalia birds emigrate at Cape Gardafui, with flocks seen from light aircraft arriving on Dhoof plain in S Oman, after sea crossing of 600 km, and many then cross a further 600 km of desert to reach Persian Gulf; singletons and loose flocks of 10-30 birds frequent in Oman from mid-Apr to mid-May, often

flying by day on broad front N or NE, or NW on Batinah coast. Recoveries of ringed birds suggest that they travel the 10,000 km from E Europe to C Africa at c. 67 km/day, and return in spring at 110 km/day.

**Status and Conservation.** Not globally threatened. European population estimated in 1990's at c. 16,000-24,000 pairs, with strongholds in Iberia (6600 pairs), and from Balkans to Belarus, Russia and Ukraine (c. 42,000 pairs); Turkish population probably c. 15,000-16,000 pairs. Remains frequent throughout much of its huge breeding range, although marked decrease in W & C Europe in last few decades, with extinction in Sweden and Germany and continuing decreases throughout whole of European range except for France, Romania, Moldova, Russia and Cyprus. Densities of 4-9 dispersed pairs/km<sup>2</sup> in prime oak and pine habitats, but species can be semi-colonial and breeding aggregations of 70 or more pairs in a circumscribed area recorded. From roadside counts in Tsavo National Park, Kenya, estimated 500,000-700,000 birds wintered there in early 1970's, and 2,000,000-3,000,000 estimated throughout E Africa, where species outnumbered all other coraciids by 5-7 times; appears equally abundant in parts of Tanzania, Namibia and Botswana; counts of 500 birds along 50 km of roadside wires in Sudan in Oct, and 5000 at Dodoma in Tanzania in Dec. Still persecuted on migration in some Mediterranean countries. Also, hundreds, perhaps thousands, shot for food every spring in Oman, where tired migrants perched conspicuously on top of low trees are easy targets; 100 or more discarded heads found near Salalah in a day. Many are wantonly, and illegally, shot in N Oman, in Kuwait, and in Farasan Is in Red Sea. Numbers of breeding pairs increased in response to occupation of nest-boxes in SW Spain. See page 368.

**Bibliography.** Abdulali (1936), Adamian & Klem (1999), Aixelá (1991), Alexander (1996b), Ali (1996), Ali & Ripley (1983), Anon. (1995a), Ash & Miskell (1980, 1998), Aspinall (1996), Avilés (1997, 1999a, 1999b), Avilés & Costillo (1997), Avilés & Parejo (1997), Avilés & Sánchez (1997), Avilés *et al.* (1998), Bannerman (1953), Barlow *et al.* (1997), Beaman & Madge (1998), Benson & Benson (1977), Benson *et al.* (1971), Blanco & González (1992), Bousquet (1999), Bracko (1986), Brown & Brown (1973), Cassola & Lovari (1979), Cave & Macdonald (1955), Christof (1991), Christy & Clarke (1998), Coles (1996), Cramp (1985), Díaz *et al.* (1997, 1999a, 1999b), Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Durango (1946), Ehrlich & Samwald (1990), Elgood *et al.* (1994), Échécoar & Hue (1964, 1978), Evans, M.I. (1994), Feare (1983), Felemban (1995), Finlayson & Tomlinson (1993), Flint *et al.* (1984), Foleh (1996), Fry *et al.* (1988), Ginn *et al.* (1989), Glutz von Blotzheim & Bauer (1980), Goodman *et al.* (1989), Gore (1990), Grimes (1987), Grimmett *et al.* (1998), Haensel (1966), Hagemeijer & Blair (1997), Handrinos & Akriotis (1997), Harrison *et al.* (1997), Heath & Evans (2000), Herremans *et al.* (1993), Herroelen (1962), Hieronimus (1994), Hirschfeld (1995), Jennings (1995), Knystautas (1993), Lewartowski (1986), Lewis & Pomeroy (1989), Lippens & Wille (1976), Lobo (1995), Lovari (1975), Mackworth-Praed & Grant (1957, 1962, 1970), Mayaud (1985), Meschini & Fraschetti (1988), Moreau (1972), Moreau & Moreau (1941b, 1946), Mukherjee (1995), Paz (1987), Penry (1990), Pinto (1983), Porter *et al.* (1996), Purroy (1997), Randall (1993), Rasmussen (1977), Richardson (1990, 1992, 1994), Robel (1988, 1990, 1991, 1993), Robel & Robel (1984, 1986), Roberts (1991), Rowan (1983), Rutgers & Norris (1977), Samwald (1989, 1994, 1996), Samwald & Samwald (1989), Saheesan (1993), Shirihai (1996), Short *et al.* (1990), Smalley (1983), Snow (1978), Snow & Perrins (1998), Sosnowski & Chmielewski (1996), Stepanyan (1990), Subramanya *et al.* (1987), Yeatman-Berthelot & Jarry (1994), Zhao Zhengjie (1995), Zimmerman *et al.* (1996).

## 8. Blue-bellied Roller

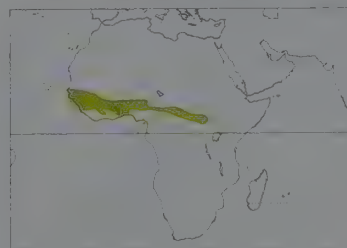
### *Coracias cyanogaster*

**French:** Rollier à ventre bleu      **German:** Opalracke      **Spanish:** Carraca Blanquiazul

**Taxonomy.** *Coracias cyanogaster* Cuvier, 1817, Java; error = Senegal.

Relationships uncertain; no obvious close allies within genus. Monotypic.

**Distribution.** Senegal and Sierra Leone to Central African Republic; also extreme N Zaire and S Sudan (between Maridi and Kajo Kaji), but very few records.



**Descriptive notes.** 28-30 cm (with streamers up to 6 cm more). A large and highly distinctive roller. Dark blue, with black back, chalky pinkish-buff head and breast, and pale azure tail and wingstripe; tail has moderately long streamers. Sexes alike. Immature similar to adult, but duller, tail without streamers.

**Habitat.** Almost restricted to mature *Isobornia* woodland; also woodland in derived savanna near rainforest zone, burnt-over clearings in rainforest near its N edges, borders of gallery forest in Guinean savanna woodland, dense woods adjacent to moist grassland, and groves of *Borassus* palms near marshes and streams.

In Sierra Leone, associated with degraded *Lophira* belt across W & C.

**Food and Feeding.** Large invertebrates and small vertebrates, also occasionally nuts of oil palm (*Elaeis guineensis*). Recorded items include mantises, grasshoppers, bugs, beetles, termites, ants, wasps, ant-lion (Myrmeleonidae) larvae, millipedes, earthworms, skinks and small snakes. In Ivory Coast, grasshoppers comprised 30% of prey, beetles (Scarabaeidae, Cerambycidae, Curculionidae) 28%, and bugs, winged termites and ants 26%. Forages from perch high up on side of a tall tree. Most prey taken from surface of ground; c. 20% are seized after short chase on wing.

**Breeding.** Lays in Apr-Jul in Senegal and Gambia, Mar-May in Sierra Leone and Feb-Sept in Ivory Coast. Monogamous or polygamous, males evidently far more numerous than females; lives all year in pairs or groups of 3-6 birds, rarely up to 20; conspicuously territorial, courtship involves 2 birds in fast chases around and above trees, the following one often breaking away and rocketing down in fast shallow flight, rolling and calling. Lays eggs in hole c. 10 m from ground in tree or palm, often too fragile for a person to climb. No other information.

**Movements.** Resident in S of range. In more arid parts of N, many are breeding visitors that spend part of the non-breeding season, Oct-Feb, among residents farther south; in N Ghana, absent in Sept-Jan.

**Status and Conservation.** Not globally threatened. In W of range mainly frequent to common, even abundant; common in NW Sierra Leone but rare in Liberia; density of 10 birds/15 ha in *Isobornia* woodland near Lamto, Ivory Coast; scarce in N Guinean zone of Ivory Coast. Increasingly less common farther E; uncommon and local in Ghana and Nigeria, probably owing to destruction of *Isobornia* woodland there.

**Bibliography.** Bannerman (1953), Barlow *et al.* (1997), Carroll (1988), Cave & Macdonald (1955), Cheke & Walsh (1996), Demy (1995), Demy *et al.* (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgood, Fry & Dowsett (1973), Elgood, Heigham *et al.* (1994), Field (1999), Fry (1980d), Fry *et al.* (1988), Gatter (1997), Giraudoux *et al.* (1988), Gore (1990), Grimes (1987), Hazevoet (1996b), Helms (1996), Jensen & Kirkeby (1980), Lamarche (1980), Louette (1981b), Mackworth-Praed & Grant (1957, 1970), Morel & Morel (1990), Moynihan (1990), Rodwell (1996), Sauvage & Rodwell (1998), Snow (1978), Thiollay (1971a, 1973b, 1985a, 1985b).

*ssp gularis*

*ssp neglectus*

9

*ssp glaucurus*

*ssp aethiopicus*

10

*ssp afer*

*spp suahelicus*

*ssp gigas*

*ssp orientalis*

11

*ssp pacificus*

*ssp waigiouensis*

*ssp solomonensis*

12



## Genus *EURYSTOMUS* Vieillot, 1816

### 9. Blue-throated Roller

#### *Eurystomus gularis*

**French:** Rolle à gorge bleue      **German:** Blaukehrlöcher      **Spanish:** Carraca Gorgiazul

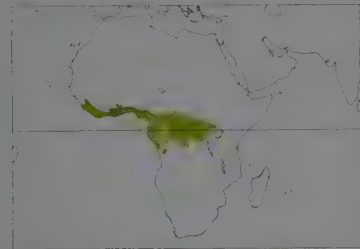
**Taxonomy.** *Eurystomus gularis* Vieillot, 1819, Sierra Leone.

Has been treated as forming a superspecies with *E. glaucurus*, the two being very similar morphologically and behaviourally; range of *E. glaucurus*, however, fully encompasses that of present species, and both probably better regarded as independent species. Races intergrade in SE Nigeria and SW Cameroon. Two subspecies recognized.

#### **Subspecies and Distribution.**

*E. g. gularis* Vieillot, 1819 - Guinea to SE Nigeria and SW Cameroon.

*E. g. neglectus* Neumann, 1908 - SE Nigeria and S Cameroon E to C Uganda, and S to NW Angola.



**Habitat.** Lowland rainforest, either undisturbed or, mainly, secondary forest with clearings, villages, hills and rivers; also small outlying forest patches, gallery forest, farms and plantations with large trees, locally savanna woodland. To some extent separated ecologically from *E. glaucurus*, although latter also uses rainforest habitat.

**Food and Feeding.** Mostly insects, taken in flight; 90% of diet ants (mainly *Crematogaster* and *Oecophylla*), with 4% beetles (Curculionidae, Elateridae, Cetonidae, Chrysomelidae, Carabidae, Tenebrionidae, Scarabaeidae, Buprestidae) and 3% termites; also shield-bugs, stink-bugs, bees, flies, crickets, cockroaches and moths. At dusk, stomachs of some individuals found to hold 750 insects weighing 39 g. Occasionally takes small fruits, centipedes and small frogs, from ground or trees. Forages above forest canopy in fast, powerful, wheeling flight like a falcon (*Falco*) or huge martin (Hirundinidae), flying out from perch 40 m up in treetop in pursuit of passing insect; uses continuous flight when exploiting hatch of flying ants or termites. Insects taken one at a time in flight. Feeds mainly in late afternoon, also well into dusk. Gathers in flocks, mixes with *E. glaucurus*.

**Breeding.** Lays in Feb-May; some evidence of breeding also in Sept and Nov. Monogamous; pair vigorously defends territory, chasing away even predatory birds; courtship involves much aerial chasing and loud calling. Nest in hole 10 m or more up in dead tree. Clutch of 2-3 eggs; incubation and fledging periods unknown.

**Movements.** Mostly resident. Poorly understood local movements recorded in Liberia and Nigeria; in Sierra Leone apparently absent from forest during rains.

**Status and Conservation.** Not globally threatened. Widespread and locally common. This species has much greater dependence than *E. glaucurus* upon tall lowland forest, suggesting that it will be at greater risk when forest is felled; but no data available on density changes in relation to man-induced habitat change. Occurs in Gola Forest Reserves (Sierra Leone), Tai Forest National Park (Ivory Coast), La Lopé National Park (Gabon), and Kibale Forest and Impenetrable Forest National Parks (Uganda).

**Bibliography.** Amadon (1953), Bannerman (1933, 1953), Britton (1980), Brown & Britton (1980), Cheke & Walsh (1996), Christy & Clarke (1994), Colston & Curry-Lindahl (1986), Dean (2000), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Dutton & Branscombe (1990), Elgoud *et al.* (1994), Field (1999), Fry *et al.* (1988), Garshore *et al.* (1995), Gatter (1997), Grimes (1987), Halleux (1994), Lamarche (1980), Lippens & Wille (1976), Louette (1981b), Mackworth-Praed & Grant (1957, 1962, 1970), Morel & Morel (1990), Pérez del Val (1996), Pinto (1983), Rand (1951), Sargeant (1993), Serle (1957), Short *et al.* (1990), Snow (1978), Thiollay (1970, 1971a, 1973b, 1985a).

### 10. Cinnamon Roller

#### *Eurystomus glaucurus*

**French:** Rolle violet      **German:** Zimtroller      **Spanish:** Carraca Picogorda  
**Other common names:** (African) Broad-billed Roller

**Taxonomy.** *Coracias glaucurus* P. L. S. Müller, 1776, Madagascar.

Has been treated as forming a superspecies with *E. gularis*, the two being very similar in morphology and behaviour; range of present species, however, subsumes that of *E. gularis*, and both are probably better considered as independent species. Race *suahelicus* intergrades with *after* and *aethiopicus* in N of its range; *aethiopicus* sometimes merged with *after* or split between that race and *suahelicus*. Birds from C & S Uganda sometimes separated as *rufobuccalis*; populations from Angola to Mozambique and Natal, averaging slightly shorter-winged than *suahelicus*, sometimes separated as *pulcherrimus*. Four subspecies recognized.

#### **Subspecies and Distribution.**

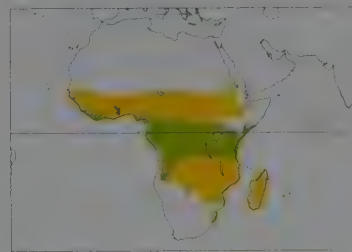
*E. g. after* (Latham, 1790) - Senegal E to C Sudan, S to Cabinda (N Angola) and W Kenya.

*E. g. glaucurus* Neumann, 1905 - SE Sudan, Ethiopia, NE Uganda and NW Kenya.

*E. g. suahelicus* Neumann, 1905 - S Somalia S to Angola, Botswana, E Transvaal and Zululand; Zanzibar and Pemba.

*E. g. glaucurus* (P. L. S. Müller, 1776) - Madagascar; migrates to E & EC Africa.

**Descriptive notes.** 27-29 cm; male 94-116 g, female 84-149 g. Nominat race has head and upperparts cinnamon-rufous, rump and uppertail-coverts blue, wings dark purple-blue with rufous lesser, me-



dian and inner greater coverts; tail shallowly forked, pale blue with blackish-blue centre and tip; chin, throat and underparts lilac, undertail-coverts greyish-blue; bill short, broad, hook-tipped and powerful, bright yellow. Differs from *E. gularis* in larger size, brighter colours, lilac (not blue) throat, mainly pale blue (not dark brown) uppertail-coverts, blue (not brown) undertail-coverts. Sexes alike. Immature rufous rather than cinnamon, and dull green-blue where adult dark blue; throat brown, rest of underparts pale grey-blue; culmen brown. Races differ in size, tone of rufous and lilac parts, and colour of tail-coverts: *after* has

slightly brighter upperparts, uppertail-coverts medium blue variably tipped brown, with central rectrices dark brown, undertail-coverts pale blue; *aethiopicus* similar but larger, with lilac on underparts brighter; *suahelicus* like *aethiopicus*, but smaller (14% smaller and nearly 30% lighter in weight than nominate) and considerably brighter, with uppertail-coverts all dull azure-blue, undertail-coverts pale blue.

**Habitat.** Woodland, wooded grassland, and cultivated country with some tall trees; also large clearings and open areas around habitations in rainforest; broad, wooded river valleys with plenty of timber, floodplains, riverine forest, wood and scrub. Typical habitats include *Brachystegia*, *Baikiaea* and *Acacia* woods, highland *Podocarpus/Juniperus* forest, hillsides, bushveld, fringing forest, and coastal wood, scrub and mangrove; sometimes in quite open grassland with only occasional stands of trees; often in built-up areas and suburban gardens. Occurs at up to 2200 m, occasionally 2500 m, in E Africa; to 1500 m in Madagascar, where it occurs in humid forest in E but is much commoner in dry country in NW & W.

**Food and Feeding.** Almost entirely insects, mostly ants and termites, also beetles, and some grasshoppers, bush-crickets, cockroaches, bees, wasps, flies; also a few spiders; lizards recorded as prey. In Ivory Coast, 80% of items were swarming winged ants and termites (mainly *Crematogaster*, *Oecophylla*, *Macrotermes* and *Pseudacanthotermes*), with 9% beetles (Curculionidae, Elateridae, Cetonidae, Scarabaeidae, Cerambycidae, Tenebrionidae, Buprestidae), 7% bugs (Lygaeidae, Pentatomidae, Plataspididae, Reduviidae, Coreidae, Jassidae, Cicadidae). Spends most of day perched on high bare branch, only rarely flying out to catch passing insect, eaten on wing after chase in buoyant, wheeling flight with fast glides; around 17:00 hours, leaves perch and congregates with others (up to c. 280) at hatching swarm of ants or termites, catching them from near ground to well above tree canopy, at rate of up to 10 insects per minute, until late dusk. Bird takes 1 item at a time, and every evening consumes 200-800.

**Breeding.** Lays in Mar-Jul in W Africa, in Jan-Apr and Sept-Nov in E Africa, and in Sept-Dec in S Africa; breeds in Oct-Dec in Madagascar. Monogamous; pair aggressively defends treetop territory of 15-30 ha, and courts with much calling and aerial chasing. Nest an unlined cavity in top of palm or in trunk or limb of large tree, occasionally in masonry. Clutch of 2-3 eggs; no information on incubation and fledging periods. Low reproductivity recorded in Ivory Coast: 569 adults near Lamto produced only 206 fledglings.

**Movements.** Nominat race in Madagascar migrates after breeding to Africa, where present throughout much of Zaire in Feb-Nov; occurs on passage in Comoro Is and in E Africa from S Kenya to NE Zimbabwe; vagrant to Aldabra and Seychelles. African races are partial migrants. In N tropics, a year-round resident or dry-season visitor during Sept-Jun at low latitudes near rainforest zone, and breeding visitor to S Guinean savanna woodland in Apr-Dec, to N Guinean zone May-Oct, and to Soudanian zone May/Jun-Sept. Migrates through Gambia in flocks. In E Africa, partially vacates Zanzibar and Pemba after breeding, but status on mainland complex. Breeding visitor during Sept-Apr to Zambia, Zimbabwe and South Africa. Vagrants recorded twice in Cape Verde Is.

**Status and Conservation.** Not globally threatened. Common and widespread in most of sub-Saharan Africa, and common throughout Madagascar except on the high plateau. Seasonal average density of 23 birds/km<sup>2</sup> in savanna-forest mosaic at Lamto, in Ivory Coast.

**Bibliography.** Anon. (1995a, 1998b), Ash & Miskell (1998), Balança & de Visscher (1996), Bannerman (1953), Barlow *et al.* (1997), Beaman & Madge (1998), Benson (1967), Benson & Benson (1977), Benson, Beamish *et al.* (1975), Benson, Brooke *et al.* (1971), Benson, Colebrook-Robjent & Williams (1976-1977), Bock (1996), Bowen (1983), Britton (1980), Brown & Britton (1980), Butchart (1988), Cave & Macdonald (1955), Cheesman & Slater (1935), Cheke & Walsh (1996), Clancey (1996), Colston & Curry-Lindahl (1986), Cramp (1985), Dean (2000), Demeey *et al.* (2000), Dowsett & Dowsett-Lemaire (1991, 1993), Dowsett & Forbes-Watson (1993), Elgoud, Fry & Dowsett (1973), Elgoud, Heigham *et al.* (1994), Field (1999), Friedmann (1930a), Fry *et al.* (1988), Gatter (1997), Ginn *et al.* (1989), Giraudoux *et al.* (1988), Gore (1990), Grimes (1987), Harrison *et al.* (1997), Hazevoet (1996b), Herroelen (1964), Jensen & Kirkeby (1980), Lamarche (1980), Langrand (1995a, 1995b), Lewis & Pomeroy (1989), Lippens & Wille (1976), Louette (1981b), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Milon *et al.* (1973), Morel & Morel (1990), Pakenham (1979), Penry (1994), Pinto (1983), Rand (1951), Sargeant (1993), Serle (1957), Short *et al.* (1990), Sinclair & Langrand (1998), Snow (1978), Snow & Perrins (1998), van Someren (1947), Sørensen *et al.* (1996), Steyn (1996b), Thiollay (1970, 1971a, 1971b, 1973b, 1985a, 1985b), Thonnerieux (1988), Urban & Brown (1971), Williams *et al.* (1986), Zimmerman *et al.* (1996).

### 11. Dollarbird

#### *Eurystomus orientalis*

**French:** Rolle oriental      **German:** Dollarvogel      **Spanish:** Carraca Oriental  
**Other common names:** Red-billed Roller, (Eastern) Broad-billed Roller

**Taxonomy.** *Coracias orientalis* Linnaeus, 1766, Java.

Forms a superspecies with *E. azureus*, with which has sometimes been treated as conspecific; breeding record of present species from Loloda Is (off NW Halmahera, and almost sympatric with range of *E. azureus*) provides additional support for their treatment as two separate species. Taxonomy and nomenclature somewhat confused, especially for continental Asian forms: nominate and race *calonyx* intergrade in areas of S China and N Indochina, and intermediate birds from N Thailand have sometimes been placed in race *deignani*; proposed race *latouchi* from NE China considered inseparable from *calonyx*; *cyanocephalus* is synonym of nominate, *abundus* is synonym of *calonyx*; Wallacean birds from S Sulawesi and Lesser Sundas, described as race *connectens*, appear intermediate between *orientalis* and *pacificus* but variable, with some individuals inseparable from latter; in past, birds of NW Australia occasionally separated as race *bravi*. Ten subspecies currently recognized.



**Subspecies and Distribution.**

*E. o. calonyx* Sharpe, 1890 - N India (Garhwal, N Assam, N Cachar) and Nepal to E China (N to Manchuria), SE Russian Far East (to lower R Amur) and Japan (Honsu to Kyushu); winters S to S Asia and Greater Sundas.

*E. o. orientalis* (Linnaeus, 1766) - NE India (S Assam), Myanmar and Indochina S to Greater Sundas, Philippines and Ryukyu Is. with single breeding record (probably this race) from Daguasuli in Loloda Is (off NW Halmahera, N Moluccas); winters S and E to N Sulawesi and Moluccas.

*E. o. laetior* Sharpe, 1890 - SW India (Western Ghats S into Kerala).

*E. o. irisi* Deraniyagala, 1950 - SC Sri Lanka.

*E. o. gigas* Stresemann, 1913 - S Andaman Is.

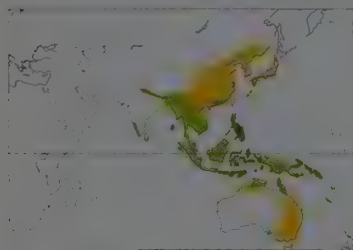
*E. o. oberholseri* Junge, 1936 - Simeulue I, off NW Sumatra.

*E. o. waigiouensis* Elliot, 1871 - New Guinea, including Karkar, Bagabag, Western Papuan Is, Yapen, Rook, Trobriand Is, D'Entrecasteaux and Louisiade Archipelagos.

*E. o. crassirostris* P. L. Selater, 1869 - Bismarck Archipelago.

*E. o. solomonensis* Sharpe, 1890 - Solomon Is (Bougainville, Buka, Feni, Guadalcanal, Ulawa, Uki and San Cristobal, probably also Nissan I).

*E. o. pacificus* (Latham, 1801) - Lesser Sundas and N & E Australia, probably also S Sulawesi and Sula Is; S populations winter N to New Guinea and Wallacea.



**Descriptive notes.** 27-32 cm; male 109-175 g and female 117-186 g (*orientalis*, *pacificus*, *solomonensis*), male 165-214 g and female 164-182 g (*waigiouensis*), female 190-205 g (*crassirostris*). A stocky roller, bull-headed and square-tailed. N nominate race dark greenish-blue, darker and more blackish on head, with blue throat; most of flight-feathers and tail dark blue, primaries with striking, large pale blue patch both above and below; bill deep and very broad at base, hook-tipped and powerful, scarlet; orbital ring and legs dark red. Differs from *E. azureus* in much greener, less purple, plumage. Sexes alike. Immature

has upperparts duller and darker, underparts slaty-blue, wing patch less brilliant blue and less well defined, throat patch greenish and ill-defined, upper mandible blackish, lower red and orange. Races differ mainly in plumage tone and in size: *calonyx* more purplish on wings, wing longer, tail shorter than nominate; *laetior* and *irisi* with head slightly blacker, blue colour brighter and more purplish, *irisi* smaller; *gigas* like nominate but with much heavier bill; *oberholseri* like nominate but head brighter, ear-coverts tinged violet, underparts clearer blue, and wing shorter but tail longer; *waigiouensis* brighter, more purplish, wing patch better defined, bill larger; *crassirostris* and *solomonensis* like previous, but bill orange-red, tail longer (especially *solomonensis*); *pacificus* with forehead, crown and ear-coverts olive-brown, paler and greyer above than nominate, much paler, more greyish-green, below.

**Habitat.** Mainly woodland, including canopy and margins of primary lowland rainforest, riparian wood, dense secondary growth, clearings, broadleaf and conifer forest, mountain taiga, peat-swamp-forest, bamboo forest; also farmland with copses and relict large trees, open country with scattered trees, and large gardens; found in *Cryptomeria* trees around old temples in Japan, and in *Melaleuca* forest and *Eucalyptus* woodland in Australia; also savanna, roadsides, parks, playing fields and wasteland. Occurs in foothills up to 1500 m, but mainly below 800 m.

**Food and Feeding.** Large, hard insects, taken in flight; mainly beetles, including chafers, carrion beetles and capricorns, also mantises, crickets, grasshoppers, shield-bugs, cicadas, sawflies, moths, ants and termites. Lizards also recorded. Up to 35 birds may congregate to exploit hatch of flying ants. Takes honeybees (*Apis*) at apiaries, and occasionally a locust or small lizard from the ground. Dismembers prey by shaking, but does not normally beat it against perch. Feeds mainly in late afternoon and towards dusk, hawking from a bare branch or telegraph wire, or repeatedly quartering ground near swarming insects, with strong, falcon-like flight and long, fast glides ending in dextrous twists and turns.

**Breeding.** Lays in Jun in N of range, May-Jun in Japan, Mar-May in India and Myanmar, Jan-Apr in Sumatra, about Nov-Mar in Papua New Guinea, and Oct-Jan in Australia; nearly fledged juvenile begging for food on Daguasuli (N Moluccas) in late Sept. Monogamous; pair hotly defends territory; courting bird rises high in air, nose-dives at speed, rolling rapidly, then flies up again to repeat sequence several times. Nest an unlined hole, often an old woodpecker or barbet hole, 8-20 m up in dead or living tree; occasionally uses nestboxes in Japan. Clutch of 3-5 eggs; in Japan, incubation period reported as 22-23 days and fledging period at least 23 days.

**Movements.** A breeding summer visitor to Russia, China and Japan in Apr-Sept, wintering S to Malaysia, N Sulawesi and Moluccas, and probably Greater Sundas; birds breeding in Australia in Sept-Mar migrate N to New Guinea, New Britain, Witu and Kai Is, Lesser Sundas and S Sulawesi; migrants probably widespread in N Melanesia, as suggested by records (subspecies unknown) outside regular breeding range, on islands of Manus and Rennell; breeding populations at lower latitudes apparently resident. Adults migrate soon after young fledge, and young follow later; migrants travel by day, but also sometimes by night (e.g. over Malaysian highlands), and often pass in impressive numbers; in many localities throughout its vast range, species is known mainly as a passage migrant, usually of considerable regularity and visibility. In Queensland a migrant was struck by an aeroplane at 2600 m, and in Irian Jaya carcasses have been found in a glacier at 4500 m.

**Status and Conservation.** Not globally threatened. Frequent throughout much of its range, and often common. In Australia, 5-14 birds/km<sup>2</sup> in *Eucalyptus* woodland, and territories every 750 m

along some creeks and streams. Formerly common in Japan, now uncommon to rare, and very local, probably as a result of habitat loss; in Philippines, too, was quite numerous in 1950's and locally to 1970's, but now uncommon, almost certainly as a result of massive deforestation that has taken place in those islands. Status of race *oberholseri* on Simeulue I requires investigation; was widespread in 1930's, but no recent records. In Sri Lanka, *irisi* was always rare and none seen for 60 years until 1950, when pair found nesting and was shot; rediscovered in Sinharaja Forest in 1979, and breeding recorded in 1980, with many subsequent sight records. Widespread and fairly common in Papua New Guinea and Solomon Is, occurring at relatively low population densities, but preferring open and degraded forest, and thus apparently secure.

**Bibliography.** Ali (1996), Ali & Ripley (1983), Ali *et al.* (1996), Austin (1948), Austin & Kuroda (1953), Baker (1948), Bechler *et al.* (1986), van Bennekom (1975), Bishop (1992), Blackman & Locke (1978), Blakers *et al.* (1984), Brazil (1991), Coates (1985), Coates & Bishop (1997), Danielsen *et al.* (1994), Darnton (1951), Deignan (1945), Dementiev & Gladkov (1951), Deraniyagala (1951a, 1951b), Dickinson *et al.* (1991), Duckworth *et al.* (1999), Dutton (2000), Engbring (1983), Étchéopar & Hué (1978), Flint *et al.* (1984), French (1957), Grimmett *et al.* (1998), Guo-Chaowen *et al.* (1988), Hadden (1981), Hale (1992), Harrison (1999), Heather & Robertson (1997), Henry (1998), Higgins (1999), Hoffmann (1985), Iida (1992), Inskipp *et al.* (1996), Isherwood *et al.* (1997), Jeyarajasingam & Pearson (1999), Jiang Wanggao & Zhu Geyang (1983), Johnstone & Storr (1998), Kennedy *et al.* (2000), King (1978/79), Knystautas (1993), Lambert & Yong (1989), Lekagul & Round (1991), MacKinnon & Phillips (1993, 2000), Madoc (1976), van Marle & Voous (1988), Mayr & Rand (1937), McClure (1998), Medway & Wells (1976), Mees (1965, 1982), Meise (1950), Nakamura & Tabata (1988), Nishioka (1932), Phillips (1978), Rabor (1977), Riley (1997a), Ripley (1942b, 1964, 1982), Robson (2000a), Rose (1997), Rutgers & Norris (1977), Scholtes (1980), Sibley (1951), Smythies (1986, 1999), Stepanyan (1990, 1995), Sugathan & Varghese (1996), Tikader (1984), Urugoda (1984), Webb (1997), Wells (1999), White & Bruce (1986), Yang Lan *et al.* (1995), Zhang Cizu *et al.* (1997), Zhao Zhengjie (1995).

## 12. Azure Roller

### *Eurystomus azureus*

**French:** Rolle azuré

**German:** Azurroller

**Spanish:** Carraca Moluqueña

**Other common names:** Purple Roller(!)/Dollarbird

**Taxonomy.** *Eurystomus azureus* G. R. Gray, 1860, Bacan.

Forms a superspecies with *E. orientalis*, with which has sometimes been treated as conspecific; breeding record of *E. orientalis* from Loloda Is (off NW Halmahera) provides additional support for their treatment as two separate species. Monotypic.

**Distribution.** Halmahera, Ternate, Tidore, Kasiruta and Bacan (N Moluccas).



**Descriptive notes.** 27-35 cm. Plumage entirely dark glossy purple-blue or inky-blue, apart from conspicuous pale azure wing patches above and below; powerful bill deep and very broad at base, hook-tipped, scarlet; orbital ring and legs dark red. Differs from *E. orientalis* in overall inky-purple plumage without green tinges. Sexes alike. Immature dull sooty-blackish, with little purple tinge, bill greyish-black with horn-yellow base, legs dusky orange.

**Habitat.** Primary and selectively logged forest, forest edge and clearings, with occasional records in coconut groves and gardens not far from forest; noted from lowlands up to 470 m

on Kasiruta, and up to 600 m on Halmahera.

**Food and Feeding.** Hawks insects, evidently much in same style as *E. orientalis*.

**Breeding.** No details known.

**Movements.** No information.

**Status and Conservation.** **VULNERABLE.** Restricted-range species; present in Northern Maluku EBA. As species was often treated as a race of *E. orientalis*, its status had not been properly investigated. Always considered uncommon, but now definitely appears to be rare, with total population estimated at only 2500-10,000 birds and decreasing. In 1980-1985, total of 9 specimens reported to have been collected in N Halmahera, mostly near Tobala, by a student of ethnography; during many protracted visits to Halmahera in 1983-1989, however, only 3 birds seen, near Peot, Sidangoli and Domoto. Not recorded on Ternate since 1945, and may be extinct there, for by 1989 its forest habitat had been reduced to relicts on upper slopes of the volcano; status on Bacan, Kasiruta and Tidore not known. Despite limited presence in semi-open areas of forest, species does not seem to adapt well to heavy degradation of habitat, and is apparently being replaced in open areas of cultivation by *E. orientalis*. In early 1990's, it was calculated that Halmahera retained forest cover over c. 90% of its surface, but latterly exploitation of forest has taken off, and timber concessions have now been granted for most of the remaining areas of forest; also, increased transmigration, settlement and conversion for agriculture or mining have become major threats to the survival of the forest and of present species. Within species' range, only one protected area exists at present, Gunung Sibela Reserve, Bacan, and this faces significant threats from agriculture and gold mining; on Halmahera, two reserves proposed, at Lalobata/Ake Tajawe and Gunung Gamkonora. Surveys required to establish true size of population; also reserves need to be established, in order to provide adequate protection for the species and its habitat.

**Bibliography.** Andrew (1992), Bishop (1992), Coates & Bishop (1997), Gibbs, D. (1990), Inskipp *et al.* (1996), Lambert (1994), Lambert & Yong (1989), Mees (1965), Scholtes (1980), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Sujatnika *et al.* (1995), White & Bruce (1986).





Class AVES  
Order CORACIIFORMES  
Suborder CORACII  
**Family BRACHYPTERACIIDAE**  
**(GROUND-ROLLERS)**



- Medium-sized terrestrial birds with full tail, short wings, and stout bill and legs.
- 24-47 cm.



- Madagascar.
- Tropical and subtropical rainforest and sub-arid thorn-scrub.
- 3 genera, 5 species, 5 taxa.
- 3 species threatened; none extinct since 1600.

### Systematics

The Coraciiformes are apparently a heterogeneous assemblage, with only a few families that are thought to be directly related to each other. Taxonomic work based on skeletal characters, by J. Cracraft in 1971 and by P. J. K. Burton in 1984, showed, however, that the ground-rollers (Brachypteraciidae), the rollers (Coraciidae) and the Cuckoo-roller (Leptosomidae) are closely related. Indeed, until fairly recently most taxonomists combined them all in a single family, merely awarding subfamily status to the three groups. Cracraft proposed elevating the ground-rollers to family status because of their profound differences in behaviour, plumage and post-cranial anatomy, and this treatment has now become widespread. It has been suggested that their sister group comprises the puffbirds (Bucconidae) and the jacamars (Galbulidae).

Cracraft suggested that the ancestors of the Leptosomidae reached Madagascar first, while the Brachypteraciidae are the result of a second invasion of roller stock from Africa. He concluded that the Brachypteraciidae and the Coraciidae are more closely related to one another, with the Leptosomidae standing apart. The morphological characters of the ground-rollers indicate that a mostly arboreal ancestor initially developed a terrestrial way of life, and then moved from the forest into sub-arid scrub. Thus, the Short-legged Ground-roller (*Brachypteracias leptosomus*), with its arboreal feeding habits, probably represents the primitive condition. Perhaps because terrestrial feeding niches were still open in primeval Madagascar, the Scaly Ground-roller (*Brachypteracias squamiger*) developed from this into a species with a more terrestrial lifestyle, as did the group represented by the genera *Atelornis* and *Uratelornis*. While the Pitta-like Ground-roller (*Atelornis pittoides*) and the Rufous-headed Ground-roller (*Atelornis crossleyi*) remained in their terrestrial rainforest habitats, the Long-tailed Ground-roller (*Uratelornis chimaera*) diverged to occupy semi-arid habitats, with subsequent morphological adaptations which caused W. Rothschild to create a monotypic genus for that species. Since C. G. Sibley and J. E. Ahlquist, in their analysis of the phylogeny and classification of the world's birds, had no tissue material available for any member of this family, they were not able to conduct the relevant DNA-DNA hybridization studies. It would appear, therefore, that Sibley and B. L. Monroe, in their complementary work on distri-

bution and taxonomy, simply accepted the close relationship of the Brachypteraciidae with the Coraciidae and the Leptosomidae.

The family Brachypteraciidae is thus represented by three genera and five extant species, all of which were described between 1833 and 1895. The classification of the ground-rollers appears now to be well established, and is generally accepted by modern taxonomists. Some early scientists, however, had placed the Short-legged Ground-roller in the genus *Colaris* and the Scaly Ground-roller in the genus *Geobiastes*, while one or both of the *Atelornis* species were sometimes assigned to the genus *Brachypteracias*.

H. E. Dresser, in 1893, named a further species as *Atelornis caeruleiceps*, the "Blue-headed Ground-roller", which he described from a single juvenile specimen. This was said to be similar to the Rufous-headed Ground-roller, but the species was never rediscovered and a formal description was never published.

Finally, one more species of ground-roller was recently described from subfossil material dating from the Holocene, and excavated at a site in south-western Madagascar. This has been named as *Brachypteracias langrandi*.

### Morphological Aspects

The ground-rollers are typified by their mostly terrestrial lifestyle and monomorphic plumage. They are generally stout-bodied birds, 25-47 cm in length, with a large head, big eyes, stout bill, short wings, and relatively long, sturdy legs adapted for cursorial habits. The name *Brachypteracias* originated from the Greek word "brakhupteros", meaning "short wing". Not surprisingly, these birds are incapable of long, sustained flight, and so usually fly only short distances. Ground-rollers weigh between about 75 g and 215 g, and males may be slightly larger than females. Sexual dimorphism in size has, however, been firmly established only for the Long-tailed Ground-roller.

The morphological characteristics of the Brachypteraciidae include ten primary feathers, twelve secondary feathers, twelve rectrices, long aftershafts on the body feathers, and powder-down patches on each side of the rump. Further features are a slightly bilobed naked oil gland, a bronchial syrinx, and slit-like nostrils. The tongue is relatively long and has a brush-like tip, which is probably an adaptation for picking up insects, the main type of



With its large head, prominent eyes, short wings, and relatively long legs, this Rufous-headed Ground-roller exhibits the typical body plan of the Brachypteraciidae. Most of the species are terrestrial, using their strong legs to run across the forest floor as they search for prey on downed logs and within leaf litter. With a body mass of about 80 g, the Rufous-headed Ground-roller is the smallest member of the family. Its most distinctive plumage feature is the black throat patch streaked with white. This species inhabits dark rainforest characterized by large trees and a dense understorey of tangled vegetation, with rotting logs and deep leaf litter on the forest floor.

[*Atelornis crossleyi*, Maromizaha Forest, eastern Madagascar. Photo: Nick Garbutt]



food for all species (see Food and Feeding). The toe arrangement is zygodactylous: the claws of the first and fourth toes are turned outwards, and those of the second and third toes are turned inwards.

Concurrent with its mostly arboreal lifestyle, the Short-legged Ground-roller has comparatively the longest wings and the shortest legs of any member of the family. All the other four have relatively short wings and long legs, and are therefore well adapted for the terrestrial habits that typify them. The two *Brachypteracias* species have a much stouter body and a much stronger bill than the other species, while the Long-tailed Ground-roller, as its name implies, has by far the longest tail.

The plumage is basically cryptic, this applying especially to the upperparts, which are mostly bronzy green and brownish. Nevertheless, some vivid colours are displayed, particularly on the head, the flight-feathers and the outer tail feathers. All brachypteraciids have a characteristic head pattern, the spectacular blue head and white throat of the Pitta-like Ground-roller being especially notable. The two species in the genus *Brachypteracias* are further distinguished by having white crescent-shaped markings on the wing-coverts, and barred or scaled underparts, while the most distinctive characteristic of both *Atelornis* species is the throat pattern. The remaining species, the Long-tailed Ground-roller, with its greatly elongated tail feathers and distinctive head pattern, bears a superficial resemblance to the Greater Roadrunner (*Geococcyx californianus*) of North America.

Juveniles of all brachypteraciids have a generally duller plumage than adults. In particular, their head and throat patterns are less distinctive.

Virtually nothing is recorded of the moult strategy of this family. All that is known is that females of the Short-legged, Scaly and Long-tailed Ground-rollers lose the tail during the nesting period.

## Habitat

All five of the ground-rollers inhabit undisturbed or only slightly disturbed native forest in Madagascar, at elevations ranging from sea-level to 2000 m. Four of the five species, the Short-legged, Scaly, Pitta-like and Rufous-headed Ground-rollers, are found almost exclusively in the evergreen rainforest in the eastern part of the island. This biogeographical zone, the Eastern Malagasy, is divided into four main vegetation types: the Sambirano humid forest, and the lowland, the mid-altitude montane and the high-altitude montane rainforests.

The Scaly Ground-roller favours lowland rainforest and is rare in mid-altitude rainforest, while the Short-legged Ground-roller inhabits both lowland and mid-altitude montane rainforest. Both are almost entirely confined to undisturbed forest with a closed canopy, and with damp areas and a deep leaf litter. The Pitta-like Ground-roller occurs from sea-level to 2000 m and is found in all major types of natural rainforest, including the Sambirano humid forest in the north-western part of the island, Amber Mountain in the north and isolated forest blocks on the Central High Plateau; it has the most extensive distribution. The Rufous-headed Ground-roller prefers higher elevations, including undisturbed mid-altitude and high-altitude montane forest with a closed canopy, a gloomy understorey with tangled vegetation, damp soil and deep leaf litter.

The four species inhabiting rainforest have distributional ranges that are roughly equivalent to the entire extent of the East Malagasy rainforest belt. In the north, all occur from at least the forest reserves of Marojejy and Anjanaharibe-Sud, surrounding the Andapa Basin, and from there extend southwards to Andohahela. The northernmost point at which the Scaly Ground-roller has been recorded is Marojejy, while the Short-legged and Rufous-headed Ground-rollers are found from the Tsaratanana Reserve southwards. As already mentioned, the

Pitta-like Ground-roller is even known from Amber Mountain, in the extreme northern part of the island.

The Long-tailed Ground-roller, however, is a geographically very restricted species. It inhabits a narrow coastal strip of sub-arid thorn-scrub and deciduous woodland in the southwestern portion of the island, an area that receives an average annual rainfall of only about 500 mm. This unique habitat type is a xerophytic spiny forest that is dominated by cactus-like *Didiereaceae* and arborescent *Euphorbiaceae* growing on sandy soils close to sea-level.

A large part of Madagascar's lowland rainforest and some of its mid-altitude montane rainforest have been transformed into grassland and degraded forest, largely as a result of slash-and-burn agriculture (see Status and Conservation). The Short-legged Ground-roller is the only brachypteraciid species which has not, so far, been reported from degraded or secondary habitats, and it may, therefore, be the least tolerant of habitat degradation. The Scaly Ground-Roller has recently been observed in secondary growth, suggesting some degree of adaptation to deterioration of habitat. The species which appears to be the most tolerant of alteration and disturbance of the forest is the Pitta-like Ground-roller, since it is able to utilize secondary forest and plantations bordering undisturbed forest. Although there have also been reports of the Rufous-headed Ground-roller in secondary forest, these records need to be substantiated. The fifth member of the family, the Long-tailed Ground-roller, will also tolerate more open, slightly degraded forest, so long as sufficient shade and leaf litter remain.

Nevertheless, all five species require undisturbed forest for their continued survival. These pristine, primary habitats constitute population sources, while degraded habitats are most likely population drains. Degraded habitats do not contain a significant proportion of the population of the Brachypteraciidae, and most ground-rollers observed in such places have been seen close to primary habitats, suggesting that the individuals involved were simply dispersing. More studies on the habitat requirements and population dynamics of this family are, however, urgently needed in order to determine these parameters and to assess their influence on the population.

## General Habits

In the words of one author, all ground-rollers are "frustratingly furtive, shy, skulking and elusive" birds, and their retiring habits are one reason for the paucity of studies on their natural history. Nevertheless, a relatively large amount of detail has been added in recent years through the extensive fieldwork of several ornithologists, including S. M. Goodman, A. F. A. Hawkins, J. E. Rakotoarisoa and R. Thorstrom.

Although all five species of ground-roller are generally diurnal, some authors have suggested that they may actively forage at twilight too, and, especially in the case of the Long-tailed Ground-roller, even during the night. The possibility of nocturnal activity does, however, require corroboration. They are terrestrial birds that forage in dense leaf litter. Foraging involves periods of attentive waiting alternating with periods of active searching. During phases of searching, the ground-roller actively climbs and jumps over obstacles, makes short runs or sally-gleans, investigates logs, and rummages through deep leaf litter. Only the Short-legged Ground-roller regularly uses trees for foraging and nesting. The remaining species occasionally perch in trees, generally on low branches but at times up to 5 m above the ground, from where they watch for prey or deliver their territorial calls.

In keeping with the mainly terrestrial lifestyle, the ground-rollers are reluctant to take to the air, preferring to freeze or to run away when alarmed. They are not capable of making extended flights, but they do sometimes move short distances in quick, direct and noisy flight in order to catch prey or to escape danger, while hawking and sally-gleaning of insects have also been recorded (see Food and Feeding). The Short-legged, Scaly and Rufous-headed Ground-rollers fly into trees to roost. Otherwise, the members of this family fly to and from their nests, but generally only after periods of intense surveying of the surroundings.

For the greater part of the year, ground-rollers appear to be solitary, but they form pairs during the breeding season, and may be seen in family groups after the young fledge. All five species are also sedentary, and they are probably territorial as well, es-

*The Long-tailed Ground-roller differs from all the other ground-rollers in inhabiting sub-arid thorn-scrub and deciduous woodland, as opposed to evergreen rainforest; it is the only member of the family that does not occur in the wetter forests of eastern Madagascar. This individual is in the midst of a bout of singing. Its song consists of a series of soft "booboooboo..." notes that differ from the guttural and often penetrating "whoops" or "boobs" given by the other species of ground-roller.*

[*Uratelornis chimaera*,  
faty, south-western  
Madagascar.  
Photo: Pete Morris]





Four species of ground-roller inhabit remnants of the evergreen rainforest that stretches from north to south across eastern Madagascar. The cryptic plumage of the aptly named Scaly Ground-roller allows it to blend in with the dense vegetation of the dark forests that it prefers. The typical foraging technique of this species consists of periods of stationary scanning followed by brief dashes across the forest floor in pursuit of invertebrates. It also probes the leaf litter and occasionally hawks insects in mid-air.

[*Brachypteracias squamiger*,  
*Maroantsetra*,  
north-eastern Madagascar.  
Photo: Dominique Halleux/  
Bios]



pecially during the breeding season. A few recorded instances of fluctuations in numerical abundance could indicate, however, that these birds do respond to climatic and other seasonal variations (see Movements). Ground-rollers remain silent during most of the year, but deliver territorial calls regularly during the breeding season, often before sunrise. While the frequency of these calls declines rapidly after sunrise, contact calls can be heard at any time throughout the entire day.

Typical body movements made by brachypteraciids include a downward bob of the head and a simultaneous upward flick of the tail during territorial calls, and a vertical raising of the tail when the bird is excited. The tail is generally held tightly closed when the bird feels threatened. Short-legged Ground-rollers often flick their wings several times before taking flight.

Ground-rollers have been observed to preen, and several species of chewing louse (Mallophaga) and tick (Metastigmata) have been found in the plumage of these birds, but little else is known about their maintenance behaviour and ectoparasite fauna. One pair of Rufous-headed Ground-rollers was watched as it bathed in a stream, and it seems likely that bathing is performed by other members of the family, too.

## Voice

Ground-rollers utter a variety of calls, the most distinctive of which are the far-carrying territorial calls. The latter are heard almost exclusively before and during the breeding season, usually from September to February. As these territorial calls are the best means of establishing the presence of ground-rollers, it seems probable that the birds have often been overlooked during the non-breeding season. Indeed, local human inhabitants are reported to believe that these birds hibernate in burrows, in the manner of certain Malagasy mammals, when not breeding (see Relationship with Man).

Vocal communication seems to be important, especially as a means of defining territories, but also in order to maintain contact within the forest. The territorial calls of the four rainforest-dwelling species are similar to one another, consisting of low, resonant and guttural notes, mostly a series of "whoop" or "boob" sounds. The corresponding calls of the Long-tailed Ground-roller are somewhat different; that species gives a series of soft notes,

"boobooboo...", or a series of chuckling "too-tuc too-tuc too-tuc..." notes. These calls are among the first ones to be heard during the morning chorus, often before sunrise. They are uttered mostly during the early morning, but sometimes also in the late afternoon, and even at night. The territorial calls are often delivered from a perch that is much higher than the level at which the species later forages. Countersinging by territorial neighbours has been noted for all five species.

The contact calls uttered by the Brachypteraciidae are much softer than their territorial calls, and are usually given by pair-members or by the members of a family. Their purpose is to enable the birds to establish, or to maintain, contact, and they are used, for example, to initiate courtship feeding. These calls can be heard throughout the day. Alarm calls are much harsher, sounding like a hissing "kwish-sh" or a loud scolding hiss, "tac tac tashhhhhhhrr". A variety of other calls has been recorded, including several associated with courtship, excitement and displays.

## Food and Feeding

Four of the five ground-roller species are almost exclusively ground-foragers that search in leaf litter for invertebrates and small vertebrates. The exception is the Short-legged Ground-roller, which prefers to forage from perches in trees, usually at lower levels, but also in the middle storey and the canopy.

The largest part of the diet of the Brachypteraciidae consists of invertebrates. Those recorded cover a wide taxonomic spectrum, and include ants, ant-lions (Myrmeleonidae), beetles and beetle larvae, butterflies, caterpillars, centipedes, cicadas, cockroaches, crabs, crickets, earthworms, flies, grasshoppers, katydids, millipedes, moths, pill-millipedes (*Sphaeroterium*), preying mantises, slugs, snails, spiders, stick-insects, wasps, woodlice and worms. In addition, some small vertebrates are taken. Among these are chameleons, frogs, geckos, lizards and snakes, as well as neonate mammals such as a tenrec (Tenrecidae) and a rat (*Rattus*). No vegetable matter has been recorded in the diet of these species.

The four ground-foraging species wait attentively, sometimes for lengthy periods, making intermittent short runs and foraging bouts, during which they actively search among logs or leaf litter. They usually pick up their prey directly from the ground, but at



Although considered to be the commonest and most widespread brachypteraciid, the Pitta-like Ground-roller is very secretive and can be difficult to locate when it is not vocalizing. This species occurs in undisturbed rainforest but also inhabits degraded second-growth forest. All ground-rollers feed mostly on invertebrates that are captured on or near the forest floor. Common prey items include ants, beetles, caterpillars, centipedes, cicadas, crickets, earthworms, grasshoppers, millipedes and spiders. Most foraging occurs during the daytime, but some species, including the Pitta-like Ground-roller, are also active at twilight and perhaps occasionally feed at night.

[*Atelornis pittoides*, eastern Madagascar. Photo: Dominique Halleux/Bios]

times they will also jump short distances to pluck small animals from overhanging leaves or branches. The Short-legged Ground-roller, for example, normally perches for long periods in a tree, now and then suddenly taking off to capture a prey item, which it picks from a branch or the ground after a brief flight; it also sally-gleans from leaves or overhanging twigs, without stopping in flight. When it spots a potential food item, it may pursue it for more than 25 m, which is a fairly considerable distance in a closed forest environment. All ground-roller species use several prey-capture techniques, such as hawking, perch-gleaning and sally-gleaning.

The Short-legged Ground-roller kills a prey item by hitting it against a branch or squeezing it with the tip of the bill, before swallowing it whole. It seems likely that this method is used by all members of the family.

## Breeding

For most of the year the ground-rollers are generally solitary, but they form pairs during the breeding season. They appear to be socially monogamous. At least during the breeding season, which extends from September to February, they defend territories, and individuals spend much time delivering territorial calls. Males of the Short-legged, Scaly and Long-tailed Ground-rollers have been observed to feed their females during the courtship period.

All species except the Short-legged Ground-roller excavate a burrow in the ground, and nest in a chamber at the end of this. The burrow is 0.3-1.2 m long, with a diameter of 7-20 cm. The nesting chamber is widened to about 20 cm, and has a shallow depression covered with dry leaves and earthy pellets. The Scaly, Pitta-like and Rufous-headed Ground-rollers usually dig their burrows in steep earth banks with overhanging vegetation, and the first of those three has been recorded to share a burrow system with an indigenous mammal, the tuft-tailed rat (*Eliurus webbi*). The Long-tailed Ground-roller, on the other hand, digs a downward-sloping burrow in consolidated sand, in areas without any grassy vegetation.

By contrast, the Short-legged Ground-roller may be the only brachypteraciid species that nests exclusively in tree cavities. According to information that came to the attention of O. Langrand, this species was said by local people to breed in burrows in the ground, although this appears rather unlikely. In fact, the nest of the Short-legged Ground-roller was not discovered by scientists until 1996. In December of that year, a pair of these birds was found nesting in a natural cavity in the dead branch of a tree, at a height of 18 m above the ground. Unfortunately, that breeding attempt failed, when the cavity was taken over by honey bees (*Apis mellifera*). In the following month, however, the same pair excavated a second nest, this time 22 m above the ground, in the soft root mass of an epiphyte. The excavation work was carried out by both pair-members, and took one week to complete. It is also of interest that the pair readily renested after loss of the first clutch.

Ground-rollers lay between October and January, but mostly in December. The clutch consists of one to four eggs, usually two. These are shiny, smooth-shelled, white and subelliptical, those of the Pitta-like Ground-roller averaging  $22 \times 27$  mm and weighing about 13 g.

The division of parental care is poorly known. Only the female seems to incubate, while the male, at least in the cases of the Short-legged and the Scaly Ground-rollers, remains in the vicinity of the nest and occasionally delivers food to the incubating female. The incubation periods of those two species are, respectively, 22-26 days and at least 18 days. The chick of the Scaly Ground-roller is described as being 5-10% feathered on hatching, but fully feathered about eight days later. The young are fed by both parents, and the nestling of the Scaly Ground-roller spends about 18 days in the nest. At the single successful nest of the Short-legged Ground-roller, the fledging period appears to have been a good deal longer, probably as much as 30 days. Fledged juveniles have been observed from November through to March, but the age of sexual maturity of the young is not known.

Almost nothing is known about the extent of nest predation suffered by ground-rollers. It would, however, seem likely that



Perched near the first nest described for the species, this male Short-legged Ground-roller is about to deliver a praying mantis to his mate, who is incubating in a tree cavity 18 m up a 30-m Weinmannia tree. Compared with other brachypteraciids, this species has longer wings, shorter legs, and a decidedly arboreal lifestyle; for these reasons, it is thought to be the most primitive living ground-roller. It often forages in the canopy, perching quietly on a branch for long periods until it spots a prey item, which it then pursues in a rapid, direct flight. Most prey is taken from tree trunks or within the foliage; captured prey items are often beaten against a branch and then swallowed whole.

[*Brachypteracias leptosomus*, Andranobé Field Station, Masoala National Park, north-eastern Madagascar. Photo: Russell Thorstrom]



the proliferation of black rats (*Rattus rattus*), even deep inside natural forest, is a potential threat affecting the breeding success of all species.

### Movements

On the basis of current information, all five ground-roller species are sedentary, and hold stable territories. Knowledge about any possible movements is, however, very rudimentary, since ground-rollers are easy to overlook during the non-breeding season. Reports of the absence of one or more of the five species from an area where they have previously been found must, therefore, be interpreted with caution.

Nevertheless, studies have shown that the abundance of Short-legged, Scaly and Pitta-like Ground-rollers varied with changes in the weather, and in one area the numbers of Long-tailed Ground-rollers were found to change seasonally. Observations of Pitta-like Ground-rollers many kilometres from the nearest forest also suggest some seasonal movement. Moreover, reports from local people that ground-rollers hibernate (see Relationship with Man) may be interpreted as indicating that the birds leave certain areas from May to August. No long-term ringing studies have been published, however, to substantiate such conclusions.

The male of the breeding pair of Short-legged Ground-rollers located in 1996 (see Breeding) was radio-tagged, and its movements were monitored over a period of three months, from October to mid-January. This male occupied a home range of 19 ha, which included all night-time roosts and the two nest-cavities. In the vertical plane, it moved between 5 m and 200 m above sea-level.

More studies on the movements of ground-rollers are urgently needed, given that migration and dispersal are important parameters for determining any conservation efforts. While the existing evidence suggests that all five species are more or less sedentary, it is possible that some short-distance movements do take place.

### Relationship with Man

Although local inhabitants are quite obviously aware of the presence of ground-rollers, as evidenced by the numerous local names given to them, it is very difficult to determine what influence, if any, these birds have on the human population of Madagascar.

The inconspicuous behaviour of the ground-rollers, and their lack of noisy calls outside the breeding season, have resulted in their being probably overlooked during much of the year. As already mentioned (see Voice, Movements), some earlier authors even reported a belief by local people that these birds hibernate during the dry austral winter in long burrows, in a similar fashion to that of certain primitive Malagasy mammals of the order Insectivora. Indeed, one of several local names for the Rufous-headed Ground-roller is "Vorona Tandranka", meaning "Tenrec-bird", thus illustrating this belief. "Tandraka" is the Malagasy name for the Common Tenrec (*Tenrec ecaudatus*), a hedgehog-like mammal that spends at least part of the period from May to October in a state of torpor in a burrow, where it survives on its fat reserves. There is, however, no real evidence to suggest that hibernation ever occurs in any of the ground-rollers.

All five ground-roller species are hunted by humans for food (see Status and Conservation). So far as is known, this is not because they are especially palatable, or are thought to possess any particular health-giving qualities, but merely because they are relatively easy targets. Like the rails (Rallidae) and most of the couas (*Coua*), which are also hunted widely in Madagascar, the ground-rollers are large-bodied birds that spend much time on the ground, and, as such, are easier to catch than are many other, more arboreal birds.

### Status and Conservation

The impact of man on the Malagasy flora and fauna has been severe. Human hunting and, perhaps, climatic changes probably led to the extinction of several bird species in historical times. At least one species of ground-roller, *Brachypteracias langrandi*,

became extinct after the Holocene, most probably because of natural environmental changes.

During the twentieth century, man's impact has intensified to alarming levels. Habitat loss and the degradation and fragmentation of forest are by far the most important factors influencing populations of ground-rollers. The loss of natural habitat has been dramatic in some areas, especially in the lowland rainforest. Slash-and-burn agriculture by subsistence farmers has the greatest negative effect on natural forest habitats, but other human activities, such as charcoal production, timber-harvesting and fuelwood-gathering, and the grazing of the understorey by cattle, also cause habitat degradation. As all ground-rollers are forest-inhabiting species, and probably require large tracts of undisturbed forest, these activities represent a serious threat to their continued survival. The species most seriously affected by forest degradation is the Long-tailed Ground-roller, since its natural habitat, sub-arid thorn-scrub, has undergone an alarming degradation rate of about 30% in the 25 years since the mid-1970's.

Hunting by humans represents a further serious threat to all ground-roller species, and the eggs of at least the Long-tailed Ground-roller are also taken. Bird-hunting is conducted mostly by people walking along forest trails that link different villages, and it is targeted at large-bodied terrestrial species such as rails, couas and ground-rollers (see Relationship with Man). Hunting of this kind may thus reduce ground-roller populations near villages and along well-used paths. In addition, dogs and introduced black rats (*Rattus rattus*) probably take a toll on ground-roller populations.

As regards conservation status, three of the five species of ground-roller are currently listed as Vulnerable. The Rufous-headed is considered Near-threatened, as, until recently, was the Pitta-like. These status categories reflect not only the restricted distribution of the Brachypteraciidae, but also the continuing destruction of their natural forest habitat. The relentless destruction, degradation and fragmentation of these forest areas result in the distribution of the four rainforest-inhabiting species becoming more and more patchy. In their favour, however, is the fact that these four species are distributed along the entire length of the Eastern Malagasy rainforest belt, and all four occur within a number of protected areas. Both the Scaly and the Rufous-headed Ground-rollers are present in twelve pro-

tected areas, while the Short-legged occurs in 14, and the Pitta-like Ground-roller can be found in as many as 18 reserves.

By contrast, the fifth species, the scrub-inhabiting Long-tailed Ground-roller, is restricted to a narrow coastal strip in south-western Madagascar. Moreover, while the four rainforest species are found in several protected areas, not a single reserve has been set up within the range of the Long-tailed Ground-roller. Human activities such as slash-and-burn agriculture, combined with charcoal production, the harvesting of timber, cattle grazing and hunting, threaten its continued survival. This species can with some justification, therefore, be considered the most threatened species of the Brachypteraciidae.

The Short-legged and the Scaly Ground-rollers are also under serious threat, since they prefer rainforest at low to middle altitudes, where levels of deforestation are much higher than those at higher altitudes. Of these two species, the Scaly Ground-roller was until recently considered the rarer, but this conclusion may be erroneous and could be a reflection of the species' more secretive nature. The Short-legged Ground-roller may even be the more threatened of the two, as it has not yet been observed in degraded forest habitats. These suboptimal habitats appear to be used, at least occasionally, by the Scaly Ground-roller, although that species has a more patchy distribution and is rarely found above 950 m, being most common in lowland rainforest below 600 m, whereas the Short-legged Ground-roller occurs at up to 1500 m. Much rainforest still remains between 800 m and 1200 m, but very little is left below 600 m.

Both the Pitta-like Ground-roller and the Rufous-headed Ground-roller can be found in high-altitude rainforest, and they appear in fact to be commoner there than in lowland rainforest. High-altitude rainforest, because of its very humid nature, its relative inaccessibility and its low timber value, is less vulnerable than that at low elevations. Moreover, both species have been observed in degraded or secondary habitats. The Rufous-headed Ground-roller was until recently considered Vulnerable, but it has now been found to be numerous within its preferred habitat of mossy forest or upper montane forest, and its range has also been found to be more extensive than previously thought. Nevertheless, despite its downgrading to Near-threatened, it is stressed that any notable decline in population or major loss of habitat could rapidly return it to the Red List. The distribution of the Pitta-like Ground-roller is rather patchy, as it occurs in isolated forest frag-



The Long-tailed Ground-roller occurs only in a strip of thorn-scrub forest 70 km by 200 km along the south-western coast of Madagascar. It is listed as Vulnerable, in part because of habitat loss in its restricted range, and also because of egg-gathering and hunting by humans and predation by introduced dogs and black rats (*Rattus rattus*). Another factor against this species is that no nature reserves have been established within its narrow range.

[*Uratelornis chimaera*, south-western Madagascar. Photo: Roland Seitre/Bios]



Invertebrates are the main prey of the Rufous-headed Ground-roller, but this individual has captured a small chameleon. With recent records in high-elevation forests, this species is now known to be commoner than previously thought. It is found in at least twelve areas that receive some form of legal protection. However, habitat destruction, especially in the form of slash-and-burn agriculture, threatens populations in the lower-elevation rainforests of eastern Madagascar.

[*Atelornis crossleyi*, eastern Madagascar.  
Photo: Dominique Halleux/Bios]



ments, such as Amber Mountain National Park and Ambohitantely Special Reserve; it does, however, have the largest range of any member of the family, and it is often found adjacent to the other species in slightly more degraded or drier forest.

To ensure the future survival of the ground-rollers, serious conservation action needs to be taken. The Malagasy government has acted to preserve biological diversity and to reduce deforestation levels. The network of protected areas is expand-

The rainforest at low and middle elevations in eastern Madagascar is highly degraded owing to logging and burning. The Short-legged Ground-roller is confined to the undisturbed portions of this diminishing habitat and is also hunted, so it is now listed as Vulnerable. Despite the seemingly dim prospects for its survival, however, it is easily overlooked and may be commoner than records indicate. In addition, the species has been found in 14 protected areas. A recent survey on the Masoala Peninsula yielded an estimate of 4 territories/km<sup>2</sup>, indicating that as many as 8800 pairs may occupy this area.

[*Brachypteracias leptosomus*, Mantadia National Park, eastern Madagascar.  
Photo: Nick Garbutt]



ing, and at the beginning of the year 2000 the total land area afforded protection approaches 3% of the island's 587,045 km<sup>2</sup>. Unfortunately, however, this network so far covers only the ranges of the four rainforest-inhabiting species, while no existing reserve is within the range of the Long-tailed Ground-roller. It is to be hoped that plans to create a new reserve in the south-western part of the island will be realized in the near future. The fact that the entire ranges of all five brachypteraciid species were recently incorporated into the system of Endemic Bird Areas established by BirdLife International should also help to focus more attention on these endemic bird species.

All species of ground-roller, in order to maintain viable populations, will need to be able to live in a landscape that is likely to become more degraded and more fragmented. There is, therefore, a requirement for many more studies to be carried out with the aim of determining each species' precise habitat requirements, population size, reproductive output, dispersal pattern, and causes of mortality. Such information will be invaluable when it comes to the establishing of detailed conservation strategies. Whether most deaths are due to humans, dogs or introduced rats, for example, would seem to be of some importance.

As a final thought, there remains the hope that the future relationship between man and ground-rollers will be a more mutually beneficial one, as, for instance, through increased ecotourism. It appears that ecotourism is already playing a significant part in the battle for the preservation of biodiversity, but the destruction and general degradation of habitat that are still apparent throughout the island will undoubtedly require specific measures to bring them properly under control.

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PLATE 30

## PLATE 30

### Genus *BRACHYPTERACIAS*

Lafresnaye, 1834

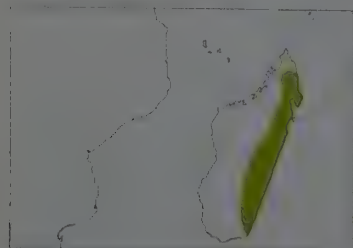
#### 1. Short-legged Ground-roller

##### *Brachypteracias leptosomus*

**French:** Brachyptérolle leptosome **German:** Bindenerdracke **Spanish:** Carraca-terrestre Patiocorta  
**Other common names:** Short-legged Pitta-roller

**Taxonomy.** *Colaris leptosomus* Lesson, 1833, Madagascar.  
**Monotypic**

**Distribution.** E half of Madagascar, from Tsaratanana Strict Nature Reserve in N to Andohahela National Park in S.



**Descriptive notes.** 30-38 cm; male 186 g, female 154 g, unsexed 183-217 g. Largest rainforest ground-roller, long-winged, short-legged, plump, with large head and puffy throat. Male bronzy green above, hindcrown and nape with violet-blue gloss, pale buffy supercilium; rump and uppertail-coverts blue-green, uppertail with dark bronzy green gloss; undertail bronzy brown, all but central pair of feathers with dark subterminal band and light-coloured tips; wing-coverts with white crescent-shaped marks outlined in black, dark primaries with whitish wingbar visible in flight; sides of face maroon-brown with white

spots, merging into brown-streaked buffy throat; white breastband, rest of underparts buff-white with brown bars, belly and vent least patterned; iris brown; stout, slightly hooked bill dark brown or horn-brown with dull yellow flange, nostrils near base of upper mandible covered by bristly

## Family BRACHYPTERACIIDAE (GROUND-ROLLERS) SPECIES ACCOUNTS

feathers, mouth-lining dull yellow; legs brownish-yellow to golden, toes greenish-yellow, claws brownish or greenish-yellow. Female differs only in slightly smaller size. Juvenile duller, browner, crown with white dots, breastband fainter, buffier below with brown-tipped (not barred) feathers on lower underparts, whitish lower mandible. **VOICE.** Territorial call a single deep "boob" repeated every 1-2 seconds for c. 4 minutes, sometimes initiated by faster version that slows until reaches normal speed, sometimes deep churring note between calls, delivered with downward-hobbing head from perch at 5-30 m, beginning prior to sunrise and only rarely heard in later morning and in evening; contact call quiet "kroo-kroo" or single "poop", softer and quieter than territorial call, given throughout day; also, soft brief purring "prrrr" and rasping squawk, associated with female soliciting courtship feeding.

**Habitat.** Inhabits humid parts of rainforest from lowlands up to middle altitudes, almost exclusively in undisturbed dark forest with large trees, damp soil and deep leaf litter, often with relatively open understorey, but found also on gentle ridge slopes with fairly dense growth of saplings, or at edge of thick tangled vegetation; absent from degraded forest. Recorded from sea-level up to 1500 m, but generally prefers lower altitudes; an old record from 1800 m is probably erroneous.

**Food and Feeding.** Most food invertebrates, including ants, ant-lions (Myrmeleonidae), beetles and their larvae, caterpillars, centipedes, cicadas, crabs, grasshoppers, katydids, millipedes, pill-millipedes (*Sphaeroterium*), preying mantises, slugs, snails, spiders, stick-insects, worms; also small vertebrates, e.g. chameleons, frogs, geckos, lizards, snakes. Possibly also takes bird eggs, as suggested by attacks on it by other species. The most arboreal ground-roller, foraging in canopy in morning, later moving to stratum between lower canopy and ground; may also be active at twilight and later. Perches motionless for long periods (up to 1 hour, average 5-10 minutes) in small tree or sapling, or pandanus or shrub, turning head only to spot prey, then moves in fast, direct and noisy flight towards new perch or towards prey; before taking flight, often ruffles feathers, flicks wings, pumps tail. Most prey captured on tree trunks or among foliage; some taken on ground or in leaf litter, which is searched with the feet, especially in areas with dense shrubs and few herbs. Sometimes takes insects by perch-gleaning or sally-gleaning. Prey killed by means of hitting against a branch or squeezing with tip of bill, after which swallowed whole.

**Breeding.** One pair laid in Dec, with replacement clutch in Jan; courtship and copulation Oct-Jan, also birds in breeding condition in Oct-Dec, and juvenile observed in early Jan. Only 2 nests known, first in natural cavity 18 m above ground in *Weinmannia* tree 30 m tall and, when that failed, second nest excavated by both sexes among root mass of epiphytes 22 m up in a 35-m *Canarium* tree; possibly also excavates in ground, where bird flushed in Sept from burrow with



entrance 10 cm wide. Clutch probably 1-2 eggs; incubation by female, fed occasionally by male, period 22-26 days; single young fledged after nestling period of c. 30 days.

**Movements.** Apparently sedentary and territorial; radio-tagged male occupied home range of 19 ha. No evidence of seasonal altitudinal movements, but numerical abundance may change locally with weather.

**Status and Conservation.** VULNERABLE. Restricted-range species; present in East Malagasy Wet Forests EBA. Uncommon, but easily overlooked; possibly more numerous than previously thought in appropriate habitat. Recorded in at least 14 protected areas; a substantial part of an important lowland site, Masoala Peninsula, is now a National Park, where there are an estimated 4 territories/km<sup>2</sup>, giving a possible 8800 pairs. Threatened by rapid habitat destruction, as most of the lowland rainforest of coastal plain already cleared by slash-and-burn agriculture. Species is also hunted.

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## 2. Scaly Ground-roller

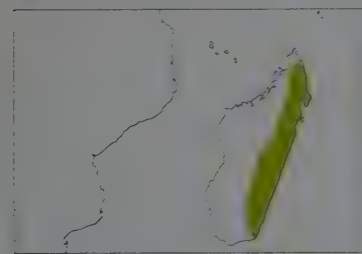
### *Brachypteracias squamiger*

**French:** Brachyptérolle écaillé **Spanish:** Carraca-terrestre Escamosa  
**German:** Schuppenerdracker  
**Other common names:** Scaled Ground-roller

**Taxonomy.** *Brachypteracias squamiger* Lafresnaye, 1838, Madagascar.

Sometimes placed in a separate genus *Geobiasies*. Species name often erroneously listed as *squamiger*, as in original description; however, genus name had initially been established (by same author) in combination with the taxa *B. leptosomus* and *B. (= Atelornis) pittoides*, using etymology "*Coracias brachypterus*", and is thus necessarily masculine, requiring agreement in gender of this species name. Monotypic.

**Distribution.** E half of Madagascar, from Marojejy National Park in N to Andohahela National Park in S.



**Descriptive notes.** 25-32 cm; male 155 g. Second largest rainforest ground-roller, plump and long-legged. Both sexes have head and underparts buffish-white with brown and black scaling, distinctive irregular black bands on central crown, behind eye and across ear-coverts below eye, belly and vent less scaly and more buffy; rufous hindcollar; bronzy green scapulars, tertials and wing-coverts, white crescent-shaped markings outlined in turquoise or blue-grey and black on lower mantle, scapulars and wing-coverts; dark brown secondaries and primaries, buffish-white wingbar visible in

flight; tail rufous with bronzy green base, outer feathers with dark subterminal band and sky-blue tip, 4 central feathers completely bronzy green; iris brown, orange-pink fleshy eyering extending to distinctive patch behind eye; stout, slightly hooked bill dull blackish-brown, slightly lighter cutting edges, nostrils near base of upper mandible covered by bristly feathers; legs pink-orange, claws dull white. Juvenile duller, buffy below, more rufous above, lightly dotted darker green wing-coverts, greenish secondaries, fainter black eyestripes. **Voice.** Territorial call a series of soft, hollow "whoop-oo" inflected slightly upwards, higher-pitched than *B. leptosomus*, repeated every 5-30 seconds, delivered from perch 0.1-5 m high during early morning and late afternoon, in bouts of up to 22 minutes; contact call single "whoop", lower and longer than territorial call; brief, muffled "ko-uh" during foraging; alarm a dry, churr and a sharp, harsh hiss, latter similar to that of Madagascar Wood-rail (*Canirallus kioioides*); harsh grating as threat; also harsh excited "kwek" notes after prey capture; and when alarmed, brief trilled "frret", sharp, raspy, hissing "kwish-sh" decreasing in volume, or soft, quiet, growling hiss.

**Habitat.** Occupies humid lowland to lower mid-altitude rainforest, with a marked predilection for undisturbed dark areas with large trees, preferring dense and tangled vegetation with damp soil and deep leaf litter, but also occurring in relatively open understorey; recently observed in secondary growth and edge habitats, suggesting it may show some tolerance to habitat degradation. May be found in drier environments than *B. leptosomus*, but often frequents damp valley bottoms. Occurs from sea-level up to 950 m, but mostly below 600 m; an old record from 1800 m is probably erroneous.

**Food and Feeding.** Invertebrates, mainly earthworms, but also ants, beetles, caterpillars, centipedes, crickets, millipedes, pill-millipedes (*Sphaeroterium*), snails and spiders; also small vertebrates, such as frogs, chameleons, lizards, and neonate mammals, e.g. a tenrec (*Tenrecidae*) and a rat (*Rattus*). More than 90% of food fed to a nestling consisted of invertebrates. Terrestrial counterpart of *B. leptosomus*; mainly searches the ground by alternating periods of attentive waiting with short runs and foraging bouts, during which investigates logs and rummages through deep leaf litter with its bill to capture animals. Perches up to 10 m high, occasionally flying short distances, or hawking flies and butterflies in air. Possibly active also at twilight and at night.

**Breeding.** Season Sept-Jan; some pairs may not breed every year. Excavates in sloping earth bank, burrow 0.5-1 m long with diameter 7-10 cm, ending in nest-chamber c. 20 cm wide and 15 cm high, lined with dead leaves and earthy pellets; recorded to co-inhabit burrow system with tuft-tailed rat (*Eliurus webbi*). Clutch 1 egg, sometimes 2; only female incubates, for at least 18 days; both parents put equal effort into feeding chick, which comes to entrance to take food; fledging period c. 18 days.

**Movements.** Generally sedentary, but in one area abundance note to change with weather.

**Status and Conservation.** VULNERABLE. Restricted-range species; present in East Malagasy Wet Forests EBA. Uncommon, but easily overlooked, and may be more common than previously believed. Occurs in at least 12 protected areas; substantial part of an important lowland site, Masoala Peninsula, recently turned into a National Park. Most serious threat is rapid habitat destruction, as most of the lowland rainforest of coastal plain already cleared by slash-and-burn agriculture. Is also hunted by humans and introduced dogs.

**Bibliography** Andriamampianina (1981), Anon. (1999b), Benson *et al.* (1976-1977), Collar & Andrew (1988), Collar & Stuart (1985), Collar *et al.* (1994), Dee (1986), Delacour (1932a), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dresser (1893, 1896), Evans *et al.* (1992), Goodman (1994a, 1994b), Goodman & Putnam (1996), Goodman & Ravokatra (1999), Goodman *et al.* (1997), Harlaub (1877), Hawkins (1999), Hawkins *et al.* (1998), King (1978/79), Langrand (1995a), Milon *et al.* (1973), Morris & Hawkins (1998), Nicoll & Langrand (1989), Powzyk (1995), Rakotomisoa (1998, 1999), Rand (1932, 1936), Safford & Duckworth (1990), Salvan (1970), Schuurman (1996), Sinclair & Langrand (1998), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Thompson & Evans (1992), Thorstrom & Watson (1997), Turner (1984).

## Genus *ATELORNIS* Pucheran, 1846

### 3. Pitta-like Ground-roller

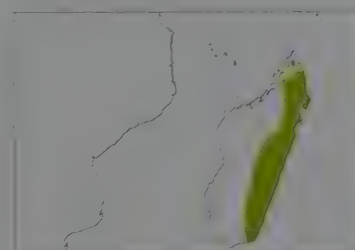
#### *Atelornis pittoides*

**French:** Brachyptérolle pittoide **Spanish:** Carraca-terrestre Cabeziazul  
**German:** Blaukopf-Erdracker  
**Other common names:** Blue-headed Ground-roller

**Taxonomy.** *Brachypteracias pittoides* Lafresnaye, 1834, Madagascar.

Monotypic.

**Distribution.** E half of Madagascar, from Amber Mountain National Park in extreme N to Andohahela National Park in extreme S, also in NE (Sambirano area) and on Central High Plateau (around Ambositantely and Ankaratra).



**Descriptive notes.** 25-29 cm; male 83-89.5 g, female 87-108 g. Second smallest ground-roller, slender and long-legged. Both sexes distinctive, with cobalt-blue head, black mask, narrow white supercilium bordered at rear above by white-dotted black feathers, feathers of forecrown and central rear crown narrowly edged brown and sparsely dotted white, conspicuous white throat bordered with blue; bronzy green upperparts except sky-blue outer tail feathers, dark brown primaries with narrow blue-white spot on primary coverts, and rufous hindcollar that extends to form second breast-band bordering the blue one; flanks rufous-orange, remaining underparts white; iris brown; slender bill black, basal nostrils partly concealed by feathers; legs dull pinkish-grey, claws pink-grey to blue-grey. Juvenile duller, black-speckled throat, blue head marked with brownish-buff, white markings more buffish, eyestripe buff-spotted brownish, pinkish lower mandible. **Voice.** Territorial call a series of penetrating, low monosyllabic hoots, "whoop", higher and shorter than *B. squamiger*, repeated every 4-10 seconds from perch at 0.5 m, mostly around dawn but also during morning or evening; quiet tucking notes as contact during foraging; alarm sharp, dry tacking notes and loud scolding hiss, "tac tac tashhhhhrrr", or short "trrrrr".

**Habitat.** Lowland to high-altitude rainforest, in undisturbed parts with dense herb layer, deep leaf litter and plentiful dead wood, also in drier forest and even secondary forest and plantations next to undisturbed forest; locally also in heavily degraded secondary forest. In study in Ambositantely Special Reserve, on Central High Plateau, found to occur in forest fragments of between 1250 ha and 28 ha, but not in smaller fragments. Sea-level to 2000 m, but commonest between 800 m and 1600 m.

**Food and Feeding.** Invertebrates, including ants, beetles, butterflies, cockroaches, other insects, and worms; also small vertebrates, e.g. chameleons. Almost exclusively terrestrial feeder, mainly searches the ground for small animals; sometimes stands motionless, then catches insects in quick sally. Active also at twilight and possibly during night.

**Breeding.** Season mainly Oct-Feb, although once observed paired in Sept. Excavates in sloping earth bank, burrow 0.5-1 m long with diameter 9-10 cm, ending in spherical chamber c. 20 cm wide and lined with dead leaves. Clutch 2-4 eggs; female incubates, male occasionally feeds female during incubation, both parents feed young; incubation and fledging periods undocumented.

**Movements.** Generally sedentary, but numbers noted to have changed seasonally with weather in one area.

**Status and Conservation.** Not globally threatened. Restricted-range species; present in East Malagasy Wet Forests EBA. Previously listed as Near-threatened, but now known to be rather common and widespread, and thought to be commonest member of the family. Present in at least 18 protected areas. Rather patchy distribution, however, and rare or absent from large areas of lowland forest, e.g. Masoala National Park. Although, as with other rainforest brachypteracids, it suffers from habitat destruction resulting from slash-and-burn agriculture, it is the most common ground-roller in slightly drier or more degraded habitats, and will even tolerate heavily degraded secondary forest; occurs in extremely high densities at certain sites, such as Manambolo Forest (between Ranomafana National Park and Andringitra National Park), particularly in a zone along the river that has been heavily degraded by cattle grazing. Appears, therefore, to be least affected of all ground-rollers by habitat degradation. Subjected to some pressure from hunting.

**Bibliography** Benson *et al.* (1976-1977), Collar & Stuart (1985, 1988), Dee (1986), Delacour (1932a), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dresser (1893, 1896), Evans *et al.* (1992), Goodman (1994a, 1994b), Goodman & Ravokatra (1999), Goodman *et al.* (1997), Griveaud (1961), Harlaub (1860, 1877), Hawkins (1999), Hawkins *et al.* (1998), Kaudern (1922), King (1978/79), Langrand (1994, 1995a), Lavauden (1937), Milon *et al.* (1973), Morris & Hawkins (1998), Rand (1936), Ravokatra *et al.* (1998), Safford & Duckworth

(1990), Salvan (1972a), Schuurman (1996), Sinclair & Langrand (1998), Thompson & Evans (1992), Thorstrom & Watson (1997), Turner (1984).

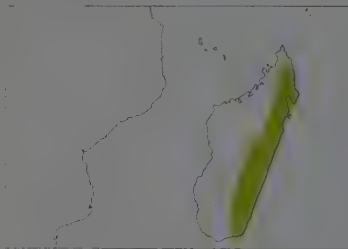
## 4. Rufous-headed Ground-roller

### *Atelornis crossleyi*

**French:** Brachyptérolle de Crossley **Spanish:** Carraca-terrestre Cabecirrufa  
**German:** Lätzchenerdracke  
**Other common names:** Crossley's Ground-roller

**Taxonomy.** *Atelornis crossleyi* Sharpe, 1875. Ampasmonhavo, Madagascar.  
Monotypic.

**Distribution.** E half of Madagascar, from Tsaratanana Strict Nature Reserve in N to Andohahela National Park in S.



**Descriptive notes.** 24–27 cm; 77.5–85 g. Smallest ground-roller, fairly slender and long-legged. Both sexes have deep rufous head and underparts, becoming lighter buffy on belly and greenish on vent, distinctive black throat and upper breast streaked with white; dark green upperparts and tail, diffuse darker centres to lower scapulars, rump and tertials, iridescent sky-blue and white patch on lesser coverts; dark brown primaries with white bases; iris brown; slender bill black, conspicuous vibrissae c. 16 mm long, basal nostrils partly concealed by feathers; legs dark brown. Juvenile generally duller, head with bluish-

purple tint, only faint black throat. **VOICE.** Territorial call a series of clear "whoop" notes, each slightly inflected, similar to call of *A. pittoides* but higher-pitched, more disyllabic, pitch highest of all rainforest ground-rollers, repeated every 3–6 seconds from perch at 0–10 m; contact call quiet croaks or very quiet clucking "bok".

**Habitat.** Humid parts of lowland to high-altitude rainforest, mostly in undisturbed dark forest, especially mossy montane forest, with large trees and dark tangled understorey vegetation, dense thickets, rotten fallen logs, damp soil and deep leaf litter. From sea-level to 2000 m, but most common between 1250 m and 1750 m. Absent along rainshadow slopes, which too dry, but possible occurrence suggested in secondary forest dominated by *Ravenala madagascariensis*, which found mainly between sea-level and 500 m.

**Food and Feeding.** Invertebrates, including ants, beetles and beetle larvae, butterflies, caterpillars, cockroaches, flies, millipedes, moths, snails and wasps. Almost exclusively terrestrial feeder, periods of standing motionless broken by periods of quick runs, climbing and jumping over obstacles, and active searches of the ground; sometimes sally-gleans insects. May be active at twilight and during night, as well as by day.

**Breeding.** Juvenile not fully grown caught in late Mar, suggesting breeding in Dec–Jan. A displaying male simultaneously bobbed head downwards and flicked tail up while calling. Excavates in sloping earth bank, burrow 0.3–0.5 m long with diameter 1.5–2 cm, ending in nest-chamber. Clutch 2 eggs; no information on incubation and fledging periods.

**Movements.** Generally sedentary; old observation that birds seemingly disappeared from an area during May–Aug, but this never verified.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Restricted-range species; present in East Malagasy Wet Forests EBA. Until recently considered rarest of the rainforest brachypteraciids, and was classified as Vulnerable, but records from a number of new sites, many of them in high mountain forests previously poorly known or unknown ornithologically, show that the species has a wider distribution and is more common than initially thought. Known to be present in at least 12 protected areas. Although it occurs over a fairly large range, distribution seems still rather patchy; no figures on densities, but c. 5 birds once heard calling within 50 m of each other. Suffers from habitat destruction caused by slash-and-burn agriculture, although less affected than the other rainforest species, which occur mostly in the more threatened lowland forest. Further census work perhaps necessary to support recent downgrading of its conservation status.

**Bibliography.** Albignac (1970), Andriamampianina (1981), Benson *et al.* (1976–1977), Collar & Andrew (1988), Collar & Stuart (1985, 1988), Collar *et al.* (1994), Dee (1986), Demey (1999), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dresser (1893), Evans *et al.* (1992), Goodman (1994a, 1994b), Goodman & Parrillo (1997), Goodman & Putnam (1996), Goodman & Ravokatra (1999), Goodman, Andrianarimisa *et al.* (1996), Goodman, Pidgeon *et al.* (1997), Griveaud (1960b, 1961), Harilaub (1877), Hawkins (1999), Hawkins *et al.* (1998), King (1978/79), Langrand (1995a), Lavauden (1932, 1937), Milon *et al.* (1973), Morris & Hawkins (1998), Nicoll & Langrand (1989), Rand (1932, 1936), Ravokatra *et al.* (1998), Safford & Duckworth (1990), Salvan (1970), Schuurman (1996), Sharpe (1875), Sinclair & Langrand (1998), Stattersfield *et al.* (1998), Turner (1984).

## Genus *URATELORNIS* Rothschild, 1895

## 5. Long-tailed Ground-roller

### *Uratelornis chimaera*

**French:** Brachyptérolle à longue queue **Spanish:** Carraca-terrestre Colilarga  
**German:** Langschwanz-Edracke

**Taxonomy.** *Uratelornis chimaera* Rothschild, 1895, Madagascar.  
Monotypic.

**Distribution.** SW Madagascar, in area bounded by R Mangoky in N, R Fiherenana in S and inland hills in E.



**Descriptive notes.** 34–47 cm (including long tail, of up to 30 cm). Highly distinctive, long-tailed, long-legged ground-roller. Male has sandy buff crown and upperparts with dark brown and black streaks; tail with c. 15–20 dark brown bars, sky-blue outer three pairs of rectrices; sky-blue on wing-coverts, including greater primary coverts, 2 vivid black and white bands along primaries and secondaries conspicuous in flight; pale buff supercilium, broad brown ear-coverts, white submoustachial stripe bordered by brown and black malar stripes which, together with black breastband, frame white throat; remaining underparts light grey,

breast almost white; iris brown; bill black; legs pale pinkish-brown. Female like male but smaller, tail shorter. Juvenile like female. **VOICE.** Territorial call a series of 6–10 soft notes, "boobooboo...", descending towards end, or series of chuckling "too-tuc too-tuc too-tuc ..." lasting 10–40 seconds and ending in harsh scratching note, similar to calls of Madagascar Coucal (*Centropus toulou*), delivered from perch 0.6–6 m high, from sunrise for c. 1 hour, sometimes during day, frequently at night; low "gu" and "guguuguu" as contact by pair-members during foraging or near nest; variety of scratching notes in excitement.

**Habitat.** Sub-arid thorn-scrub and deciduous woodland dominated by cactus-like *Didiereaceae* (especially *Didierea madagascariensis*), arborescent *Euphorbiaceae* (especially *Euphorbia stenoclada*) and baobabs (*Adansonia*), on sandy soils, and with deep leaf litter. Tolerates more open, slightly degraded forest if shade and leaf litter present, but absent from *Didierea*-covered dunes, where probably too little shade and soil too loose for excavating nest. Occurs from sea-level to 100 m.

**Food and Feeding.** Invertebrates, such as ants, beetles, butterflies, caterpillars, cockroaches, grasshoppers, woodlice, and worms. Almost exclusively terrestrial feeder, alternates motionless periods with periods of active searching, rummaging through deep leaf litter beneath bushes and trees with its bill as it searches for small animals; runs powerfully; poor flier, but occasionally hawks butterflies in air. Often active at twilight and during the night, as well as by day.

**Breeding.** Season Oct–Jan, from start of rainy season; almost fully grown juvenile observed in late Nov, and 3 full-grown juveniles in late Dec. Male sometimes feeds female, even before egg-laying. Both partners use bill and feet to excavate in flat or slightly sloping consolidated sand free of grassy vegetation, downward-sloping burrow c. 0.8–1.2 m long and 8 cm in diameter, ending in nest-chamber c. 20 cm in diameter and lined with dry vegetation. Clutch 2–4 eggs; no information on incubation and fledging periods. Post-fledging, family groups of 4–5 birds observed.

**Movements.** Generally sedentary; appeared to occur seasonally in one area, being generally absent in May–Aug.

**Status and Conservation.** VULNERABLE. Restricted-range species; present in South Malagasy Spiny Forests EBA. Uncommon; probably the rarest and most endangered brachypteraciid because of its restricted range, possible migratory behaviour, and lack of protected areas within its range. Occurs only in narrow coastal strip, at most 70 km wide and 200 km long. Conservation areas for this region proposed, but not yet implemented. Is nevertheless common in suitable habitat, and record of 7 territorial birds calling simultaneously. Some tolerance to disturbance by roaming cattle, and can be seen close to villages; population density, however, appears to be positively correlated with distance to nearest road, suggesting negative effect of local human populations. Most serious threat is rapid habitat destruction from human activities such as slash-and-burn agriculture, charcoal production, timber-harvesting for local and commercial use, and cattle grazing; probably also hunted by humans and dogs, and nests perhaps preyed on by introduced black rats (*Rattus rattus*).  
**Bibliography.** Appert (1968b), Collar & Andrew (1988), Collar & Stuart (1985, 1988), Collar *et al.* (1994), Dee (1986), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Griveaud (1960a), King (1978/79), Langrand (1995a), Lavauden (1937), Milon *et al.* (1973), Morris & Hawkins (1998), Rand (1932, 1936), Safford & Duckworth (1990), Salvan (1970), Schuurman (1996), Seddon *et al.* (2000), Seitre (1997), Sinclair & Langrand (1998), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Turner (1984).





## Class AVES

## Order CORACIIFORMES

## Suborder CORACII

## Family LEPTOSOMIDAE (CUCKOO-ROLLER)



- Medium-sized arboreal birds with disproportionately large head, round body and short legs.
- 38-50 cm.



- Madagascar and Comoro Is.
- Tropical and subtropical forest and secondary habitats.
- 1 genus, 1 species, 3 taxa.
- No species threatened; none extinct since 1600.

## Systematics

The Cuckoo-roller (*Leptosomus discolor*), which is also commonly known, even to English-speakers, by its French name of Courol, is restricted to Madagascar and the Comoro Islands. It forms a monospecific genus placed in its own family, with three subspecies currently recognized. The nominate form *discolor* is found in Madagascar, Mohéli (now known as Mwali) and Mayotte (Maore), while *gracilis* occurs on Grand Comoro (Ngazidja) and *intermedius* on Anjouan (Ndzuani). The last form has sometimes been referred to as the subspecies *anjouanensis*, but this name is now considered a junior synonym of *intermedius*. As the race on Grand Comoro differs noticeably from the others (see Morphological Aspects), it has been suggested that it should be accorded full species status, but the somewhat intermediate features of the aptly named Anjouan race argue against this.

The placement of this genus with regard to the higher orders of avian taxonomy has had a varied history. When first described, in 1783, the Cuckoo-roller was considered to be a cuckoo (Cuculidae), and since that time it has often been placed with the rollers in the Coraciidae, usually in its own subfamily. The first critical morphological study of the genus was published in 1865, and was based largely on feather, foot, tongue and bone structures. The principal findings of that study showed that *Leptosomus* was not a *Cuculus* cuckoo, as it had originally been thought to be, but rather that it should be placed in its own family, near the Coraciidae. Subsequent studies on the muscular system have corroborated this arrangement. These have demonstrated that the Cuckoo-roller shares numerous features with the typical coraciid rollers of the genus *Coracias*, although *Leptosomus* and *Coracias* exhibit distinct differences in the characters of the skeleton, the syrinx and the powder-downs. The Cuckoo-roller's ear-bone structure resembles that of the rollers, the ground-rollers (Brachypteraciidae) and the hornbills (Bucerotidae) in that it shares the primitive form of their stapes. On this basis, all these groups have been united in the Coraciiformes, an order which also includes the kingfishers (Alcedinidae), todies (Todidae), motmots (Momotidae), bee-eaters (Meropidae), hoopoes (Upupidae) and woodhoopoes (Phoeniculidae).

In more recent works on the higher-level arrangements of birds, using such varied characters as their feeding apparatus, DNA-DNA hybridization data, and skeleton and muscle structure, the Cuckoo-roller is almost universally considered to represent a monospecific group closely allied to the other coraciiforms.

It is generally placed in a suborder (Coracii), together with the Coraciidae and the Brachypteraciidae, and either in the same superfamily as those or in a superfamily of its own.

Apparently, there is no fossil record for the genus *Leptosomus*, although it has been found as recent subfossil material in excavations at sites in Madagascar and the Comoros.

In the past, the family name has frequently been given as Leptosomatidae. However, the stem of this name is based on acceptance of the invalid genus name *Leptosoma*, and under currently accepted nomenclature the family name must be Leptosomidae.

## Morphological Aspects

The generic name *Leptosomus* is derived from Greek words meaning "delicate body", which is to some extent a misnomer, since the basic body plan of the Cuckoo-roller is by no means delicate. In fact, when viewing this bird in the wild, one is impressed by its distinctly heavy body form and its massive head. Perhaps this ref-



The Cuckoo-roller is a noisy bird and its mournful call is commonly heard in the breeding season as it circles and glides for long periods over the forests of the Indian Ocean islands to which is restricted. It was originally classified as a cuckoo (Cuculidae) until morphological analysis placed it alongside the rollers (Coraciidae), where it is usually awarded a family of its own.

[*Leptosomus discolor*, Madagascar.  
Photo: Roland Seitre/Bios]



As the Cuckoo-roller requires large trees for nesting, roosting and perching, and to provide the organisms upon which it feeds, it is usually considered a forest bird. It frequents a wide variety of habitat types, ranging from the montane rainforest seen here to lowland rainforest, deciduous forest, gallery forest, the dry spiny forests of the south-west, littoral scrub, parkland and plantations, and it also ventures out over more open terrain. This generalist strategy and tolerance of land-use changes has allowed the species to remain common and widespread despite the destruction of Madagascar's forests.

[*Leptosomus discolor*,  
Mantadia National Park,  
Madagascar.  
Photo: Nick Garbutt]



erence is most appropriate to its distinctly short and delicate legs. The specific name *discolor*, meaning "of different colours", refers to the pronounced sexual dichromatism in the species' plumage. The eye appears set far back on the head, the bill is stoutish and broad-based, with a slightly hooked and serrated tip, the wings are long and ample, and the tail is moderately long.

Varying opinions have been expressed by different authors on the foot structure of the Cuckoo-roller. On the basis of an early anatomical study, it was noted that the structure of the leptosomid foot differed from the zygodactyl structure of, for example, the cuckoos and the puffbirds (Bucconidae) in that the fourth toe extends "laterally, rather more behind than in front". Recent observations of captive Cuckoo-rollers, however, indicated that the birds definitely perched "in zygodactylous manner under all conditions".

The Cuckoo-roller's less obvious structural features include slit-like nostrils, a bronchial syrinx, a slightly bilobed naked oil-gland, and long aftershafts on the body feathers. A pair of powder-down patches, one on each side of the rump, between the dorsal and femoral feather tracts, may be responsible for the characteristic greyish bloom of the plumage.

There are ten primary feathers, twelve secondary feathers and twelve tail feathers. The feathers of the lore initially face forwards and then curve upwards and back, thereby extending the forehead feathering over the base of the bill and increasing the apparent size of the head. A short, blunt crest on the rear of the crown further enhances the bird's big-headed appearance.

The plumage colouring of the adult male comprises a grey head, with a thin black band through the eye, and a black cap. The metallic greenish back, tail and upperwing-coverts have a violet sheen, while the underbody is grey and white. The flight-feathers are deep dark blue, and the underwing is white with a dark wingtip. The feet are brown or dull orange. The adult female differs dramatically from the male, being mainly brown around the head and mantle and having heavily spotted underparts. It has been proposed that adult males in Madagascar have a non-breeding plumage similar to the duller brown of the adult females, but there seems to be no evidence to support this.

Several views have been presented in the literature with regard to sexual dimorphism in the plumage of juvenile Cuckoo-rollers. For Malagasy populations, it has been reported that

juveniles are similar to adult females in plumage pattern, but are generally duller in colour. At least one author has mentioned, though without giving any details, that the two sexes could be differentiated at fledging by their plumage coloration, and a recent study of captive juveniles of the subspecies *gracilis*, taken from a nest on Grand Comoro, did reveal clear patterns of dimorphism that paralleled differences between adult males and adult females. There is some evidence, too, that the juvenile of the Anjouan subspecies *intermedius* shows sexual dimorphism.

The Grand Comoro subspecies *gracilis* is noticeably smaller than the other two, being typically about 38 cm long, rather than around 43 cm. In addition, the male is whiter underneath, and the female's tail is bright chestnut-red rather than dull brown in coloration. On this basis, and because of its differing vocalizations (see Voice), this population was elevated to the status of a full species by I. Sinclair and O. Langrand in their 1998 treatment of the birds of the Indian Ocean islands.

The few data on weight that are available for the subspecies *gracilis* reflect its smaller size, and include an adult male at 160 g and an adult female at 196 g. Four adult males of the nominate subspecies weighed, respectively, 192 g, 205 g (two birds) and 219 g; an unsexed adult weighed 222 g, and an unsexed subadult 240 g. The data for *intermedius* include a female, which may have been ready to lay eggs, at 270 g.

Some data on the Cuckoo-roller's bare-part colours suggest that these, too, may vary geographically, but the information available is insufficient for any firm conclusions to be drawn on this. It is quite possible that the differences may be the result of no more than individual variation.

## Habitat

The Cuckoo-roller occupies a wide variety of habitats, including both natural zones and those created by or altered by man, but virtually all aspects of its life-cycle occur in forest, or at least in areas which still contain large trees. It breeds in tree hollows, and the sites that it uses for roosting and perching are invariably in trees, while the bird seems to hunt exclusively in forest and to feed on forest-dwelling organisms. The species would appear to be essentially forest-dependent.

In Madagascar, the Cuckoo-roller occurs along the complete length of the island in a variety of habitats, including rainforest, littoral forest, spiny bush-forest, deciduous forest, gallery forest and tree plantations, as well as more open parkland. It is also present in heavily degraded environments, which are, in most cases, relatively close to forested habitat (but see Movements), although in south-east Madagascar it has been observed in agricultural areas several kilometres from any forest. The altitudinal range from which the bird is known extends from near sea-level up to the high mountain zones at 2000 m.

In the Comoros, Cuckoo-rollers are found on all the major islands, particularly in forested zones and in isolated forest fragments. They have been reported from sea-level to about 1500 m. On certain islands, however, the species' distribution appears to be very patchy.

## General Habits

Although the Cuckoo-roller can be tame and confiding, it will remain motionless for long periods and can, therefore, be difficult to see, particularly in the dense canopy of the rainforest. Its presence is often disclosed through its distinctive vocalizations (see Voice), and small groups of calling birds are often seen flying over the forest. Indeed, one of the most characteristic features of the Cuckoo-roller is its swooping and undulating or floating flight, generated through deep, slow and methodical wingbeats.

Except for a few studies on the breeding and feeding habits of the Cuckoo-roller in Madagascar and the Comoros, carried out by A. Forbes-Watson and O. Appert in the 1960's, little information is available about the species' natural history. This is due, at least in part, to its utilization of the middle and upper portions of the forest canopy, where observations from the ground are frequently difficult. Cuckoo-rollers are more often than not observed in twos, which presumably represent monogamous pairs, but they can also be seen in parties of up to ten individuals, calling as they fly over the forest canopy. To a large extent, the social organization and the context of these congregations are not known; during certain seasons they may represent territorial encounters, family groups or, perhaps, even foraging flocks. The birds can be heard calling at night, but it is not clear whether any truly nocturnal activity is normal.

A characteristic feature of forest-dwelling birds in Madagascar is the formation of mixed-species flocks, particularly outside the breeding season. These flocks are generally to be found in the lower forest strata. There is little evidence that the Cuckoo-roller

ever participates in these flocks. This may be due in part to its perch-and-wait and active aerial foraging techniques, neither method being conducive either to the types of movements of multi-species flocks or to the stratum of the forest in which they occur.

Little information is available on the natural predators of the Cuckoo-roller. In the dry deciduous forest of western Madagascar, bone fragments of one individual were found in the faeces of an endemic carnivore, the fossa (*Cryptoprocta ferox*), and it seems likely that certain raptors and other predators raid the species' nests (see Breeding). Any anti-predator strategies employed by the Cuckoo-roller, however, remain unknown.

## Voice

The flight calls of this species are one of the characteristic avian sounds of Madagascar forest, and the distinctive call is often the simplest means by which to establish the species' presence within a forested zone (see Status and Conservation). Cuckoo-rollers can be extremely loud, and often utter a very typical, plaintive "whee-oo" or "rhee-oo" whistling cry that rises in pitch in the middle. This call is delivered repeatedly during a gliding flight over the forest canopy, and is sometimes terminated by a harsh "wha-ha-ha-ha". The same sequence is occasionally given by birds perched in trees, when the swollen or inflated throat is clearly visible.

The vocalizations of the various populations appear not to differ from one another, with the exception of the Grand Comoro race *gracilis*. The calls of this form are reported to be faster and higher-pitched than those of populations living in the rest of the Comoros and in Madagascar.

Several calls have been described from breeding pairs that perhaps do not occur in other contexts. Thus, various whistling calls have been heard from flying birds as they approach perches near the nest: these include a soft, starling-like, descending "kriuuu", a soft plaintive "trooo" and a soft "hiyer".

## Food and Feeding

Little quantified information is yet available on the Cuckoo-roller's diet, but what data there are suggest that chameleons (*Furcifer*, *Calumma*) may make up a significant proportion of it. Of the stomachs of 23 individuals collected during the 1929-1931 Franco-Anglo-Américaine mission to Madagascar, five contained remains of chameleons 8-14 cm long; locusts were found in twelve stomachs, caterpillars in nine, and various types of beetle (Coleoptera) in one, while seven stomachs held other large insects. The stomach of this species has often been found to be lined with the "fur of hairy caterpillars", and the bird has also been reported to eat grasshoppers (Orthoptera), cicadas (Hemiptera), stick-insects (Phasmida) and fringed geckos (*Uroplatus*). Specimens collected in dry forest near Mampikony in western Madagascar and near Sakaraha, in the south-west, were found to have consumed beetles, grasshoppers or locusts, and caterpillars. The stomach of an immature from Sakaraha contained remnants of a 20-cm chameleon. During Appert's observations at nests in the south-west of Madagascar, the principal foods brought in by the adults were hairy caterpillars and cicadas, and only once was the female observed to carry a chameleon. The diet is similar on the Comoros, and there the Cuckoo-roller has been characterized as eating principally chameleons and large-bodied insects.

The general foraging technique of the Cuckoo-roller involves perching motionless, generally in the upper portions of the forest canopy, watching and waiting, and then, when a potential prey item is observed, making a short sallying flight. This species also hunts by active aerial foraging, again in the upper part of the forest canopy. Prey is generally captured with the massive bill. The feet and claws are proportionately small and weak, and of little use in subduing prey. In some cases, the bird will fly with the live or stunned prey in its bill to a nearby perch, there dispatching the animal by beating it against a tree trunk or branch.

*Female Cuckoo-rollers differ greatly from males, being buffy brown, strongly barred and spotted darker brown. This female is of the nominate form from Madagascar, Mohéli (Mwali) and Mayotte (Maore). The Grande Comoro race gracilis, with paler underparts in both sexes, more uniform upperparts in the female and somewhat different vocalizations, is sometimes treated as a separate species.*

[*Leptosomus discolor*, Mayotte, Comores.  
Photo: Roland Seitre/Bios]





Judging by the scant anecdotal evidence available and the stomach contents of specimens, the Cuckoo-roller seems to feed mainly on invertebrates such as beetles, crickets, stick-insects, cicadas and larval moths. Another important food source is vertebrates such as chameleons and geckos. The Cuckoo-roller perches quietly for long periods in the canopy of forests until prey is sighted, upon which it executes a short sally to seize it with its bill. Note the distinctively large head, with the eye appearing to be set oddly far back.

[*Leptosomus discolor*, Mayotte, Comores.  
Photo: Roland Seitre/Bios]



## Breeding

The Cuckoo-roller's nest was unknown to science until 1965, when Forbes-Watson discovered one during a visit to the island of Mayotte, in the Comoros. Much of our knowledge of the species' nesting habits is based on his study, and on data subsequently gathered by Appert at two nests in south-west Madagascar. There seems to have been nothing published on the breeding of the species since that time.

Apparently, the breeding season varies little, even given the considerable differences in the types of habitat which the species occupies and the longitudinal extent of its range, which covers 14 degrees from 11° S to 25° S. Once again, however, few data are available on the timing of breeding, and in numerous cases the season has had to be inferred from the condition of the gonads of collected specimens. Thus, in Madagascar, the nesting season is calculated to be between November and December, and on the Comoros it appears to start in mid-September.

In the literature on the birds of the Malagasy Region published in the middle of the nineteenth century, it was suggested that this species was polyandrous. There appears, however, to be no evidence to support this claim. In the case of the nests watched by Forbes-Watson and Appert, only a single male was observed attending the breeding female.

The nesting site is in a natural tree cavity, about 4-6 m off the ground. No material is added to the nest-chamber, the eggs being laid directly on to the bottom of the cavity. The clutch appears usually to be of four or five eggs, whitish in colour, slightly tinted with beige-green, and measuring on average 45.2 × 38.4 mm. The incubation period is at least 20 days. The nestlings are covered with long white down, and they remain in the nest for about 30 days before fledging.

Incubation is undertaken by the female, starting when the first egg is laid, and during this period the male provides nourishment for her at the nest. Once the young have hatched, generally only the female visits them with food. It is not clear whether both sexes participate in hunting at this time or whether the male may be largely responsible, transferring prey to the female in the general vicinity of the nest. Nestlings have been seen to be fed on apparently whole chameleons, about 10 cm in length, each chick receiving an estimated six chameleons per day. The nest-cavity has a strong musky smell, reminiscent of the nesting sites of the Hoopoe (*Upupa epops*). Apparently, the faeces produced by the young are

not removed from the nest-hole by the adults, and the young do not attempt to direct their faeces outside the cavity. When disturbed in the nest, the young have a remarkable threat display which is reminiscent of that of nestling owls (*Strigidae*): they bow down, gaping and calling, and then snap the bill shut.

Although, in western Madagascar, this species has been identified as having been eaten by the fossa, a carnivorous mammal that preys mostly on small mammals, the details of how the bird was taken are unknown. Presumably, various birds of prey will feed on Cuckoo-rollers and their eggs and nestlings, a likely example being the Madagascar Harrier-hawk (*Polyboroides radiatus*), which probes with its long tarsi into holes, nooks and crannies of trees for potential prey. Various species of snake and large diurnal species of lemur (*Lemuridae*) are known to raid birds' nests and to feed on their contents, and the Cuckoo-roller may occasionally be subject to such predation.

This species has on several occasions been observed performing an aerial display in groups of up to ten individuals, males usually predominating. This display normally consists of the birds flying just above the forest canopy and uttering a piercing "dree-o" call three times. In one instance, four males, including one subadult, were watched for about 25 minutes as, calling continuously, they flew around a tree in which a female was perched; she responded with the same call as that given by the males. The function or significance of this behaviour is not clear, but it may be part of a courtship display, or it could, perhaps, even be territorial in nature.

## Movements

There is no definitive study of the Cuckoo-roller's migratory movements. It has been hypothesized that, during the rainy season, the populations breeding in eastern Madagascar move westwards to the central high plateau, and then on to the western region, but there is little evidence to suggest that this is the case. During the breeding season, these birds are very obvious, owing largely to their characteristic loud calling. Once the nesting season has ended, however, and the birds are no longer calling regularly, one is left with the impression that the local population is no longer present.

What little is known of the species' movements suggests a pattern that might best be referred to as meandering, rather than migratory. Individuals have been observed outside the breeding



The Cuckoo-roller is apparently monogamous. The female lays 4-5 eggs in natural tree cavities, roughly 4-6 m above ground level, and incubates them herself, while the male brings regular gifts of food. After around 20 days, the chicks hatch and develop long white down, remaining in the cavity until they fledge about a month later. If they are disturbed before this time, nestlings bow down towards the intruder, gaping and calling, and then snap the bill closed, a threatening defence strategy reminiscent of young owls (Strigidae).

[*Leptosomus discolor*, Mayotte, Comores. Photo: A. Forbes-Watson/VIREO]

season in non-forested areas of the central high plateau, as, for example, in Madagascar's capital city, Antananarivo, a considerable distance from any remnant forest blocks.

It seems that the home range of the species may encompass large areas, within which it moves short distances when the need arises. In Madagascar, the Cuckoo-roller has been observed crossing open areas between patches of forest. In the south-eastern portion of the island, in a zone with an abrupt and dramatic ecotone between dry and humid forest types, it has been seen flying and calling above the edge of the rainforest and then dropping down at least 100 m in elevation to the spiny forest several kilometres away. Such movements, however, can hardly be considered to represent migration in any form.

### Relationship with Man

The Cuckoo-roller's tameness, even at the nest, suggests that it is rather unlikely that it is ever molested by local people. Indeed, among certain cultural groups living in Madagascar, it is considered to be a bird of good omen. After a period of heavy rain, or the violent winds of a cyclone, the cry of this species is regarded as a harbinger of clear weather.

Since the Cuckoo-roller is often observed in pairs, it is a traditional native Malagasy belief that it represents the union of a couple, and the bird is therefore regarded as being *l'oiseau d'amour*. Among the Sakalava of western Madagascar, portions of the Cuckoo-roller's body, such as its eyes and plumes, are used for love potions and aphrodisiacs. These concoctions are utilized in a variety of ways: the bird's fat is applied as an ointment, and various portions are consumed orally.

On the other hand, there is a conflicting report on the role of the species in Sakalava folklore. This states that people are afraid of this bird, because it foretells death if it flies over the roof of the house.

### Status and Conservation

Madagascar is faced with an environmental crisis associated with the disappearance of its once extensive areas of relatively intact

forest. All of Madagascar's major natural forest formations in which the Cuckoo-roller occurs have declined drastically in the past few decades. These include rainforest, deciduous forest and dry forest.

The Cuckoo-roller's distribution in Madagascar is extensive, and the natural habitat needed for its maintenance is still present. There is little targeted human pressure, such as hunting, or exploitation for associated products. On the Comoros, occasional human disturbance of nesting sites occurs, but the importance of this type of pressure as a threat to the species is difficult to assess.

Populations in Madagascar are able to persist in relatively small forest fragments. For example, in the Réserve Spéciale d'Ambohitantely on the central high plateau, the birds have been found in areas of fragmented forest as small as 12 ha in extent. Furthermore, the species seems to have no inhibition about crossing the savanna-like areas that now separate the remaining patches of forest. Densities are, however, generally higher in intact forest than they are in degraded habitats. Given these factors, it is apparent that the Cuckoo-roller does not face any greater threat than do other widely distributed forest-dwelling animals in Madagascar. Some areas with significant populations of the species include those broad expanses of forest associated with reserves such as Marojejy, Zahamena, Andringitra and Andohahela. It has also been said that it may be easier to observe this bird in dry forest in the western part of the island, as at Zombitse-Vohibasia National Park and Ampijoroa Forest Station, but whether this is because the species is comparatively more numerous there is not clear.

The species' vocalizations (see Voice) provide an excellent means of establishing its presence in an area. A lack of calling, however, does not necessarily imply its absence, for calling is less frequent outside the breeding season. Further, it is difficult to establish density estimates during the breeding season using techniques such as point counts, largely because of the great distances over which the calls carry and the fact that Cuckoo-rollers regularly call in flight.

The Grand Comoro form *gracilis*, proposed as a full species (see Systematics), does not seem to be spread across that whole island but, rather, it occurs in forested zones along certain slopes of Mount Karthala. It has been estimated to number about 100 pairs. With so small a total population, confined to one relatively small island, this taxon would seem to be in need of a full census.





## Family LEPTOSOMIDAE (CUCKOO-ROLLER) SPECIES ACCOUNTS

## PLATE 31

### Genus *LEPTOSOMUS* Vieillot, 1816

#### Cuckoo-roller

#### *Leptosomus discolor*

French: Courol

German: Kuro!

Spanish: Carraca Curo!

Other common names: Courol

**Taxonomy.** *Cuculus discolor* Hermann, 1783, Madagascar.

Sometimes considered to belong within Coraciidae, where typically awarded its own separate sub-family. Race *gracilis* sometimes considered a separate species, on basis of differences in size, plumage and voice; however, *intermedius* appears intermediate in plumage and may thus link the other two. Proposed race *anjouanensis* synonymous with *intermedius*. Three subspecies currently recognized.

#### **Subspecies and Distribution.**

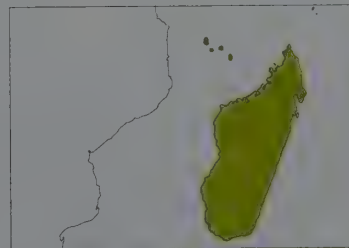
*L. d. gracilis* Milne-Edwards & Oustalet, 1885 - Grand Comoro (Ngazidja).

*L. d. intermedius* Hartert & Neumann, 1924 - Anjouan (Ndzuani).

*L. d. discolor* (Hermann, 1783) - Mohéli (Mwali) and Mayotte (Maore), and Madagascar.

**Descriptive notes.** 38-50 cm; 192-270 g. Male of nominate race has grey head, with thin black band running through eye and connecting to black cap; metallic green upperparts, with purple gloss varying according to angle of light; grey and white below. Female has head and neck brown with darker barring; back, upperwing-coverts and tail dark brown, marked with chestnut; underparts white to buff, with tan tinge on throat, boldly and irregularly spotted dark brown. Juvenile reportedly like female but duller; possibly showing sexually dimorphic characters, though this uncertain. Races differ in size and plumage coloration: *gracilis* distinctly smaller than nominate, male with clearly demarcated bluish-grey throat and upper breast contrasting sharply with white underside, female has uppertail cinnamon and spotting on underparts variable but generally more intense on breast, juvenile known to be sexually dimorphic; male *intermedius* similar to male *gracilis*, female and young birds generally darker, and distinguished by dark brown tail.

**Habitat.** Occupies a wide variety of habitats, including rainforest, littoral forest, spiny bush-forest, deciduous forest, gallery forest, tree plantations, parkland and open habitats. Recorded from near sea-level up to 2000 m.



**Food and Feeding.** Largely carnivorous, eating a variety of invertebrates (mostly insects), as well as reptiles, especially chameleons (*Furcifer*, *Calumma*). Normally hunts by means of perch-and-sally or by active aerial foraging.

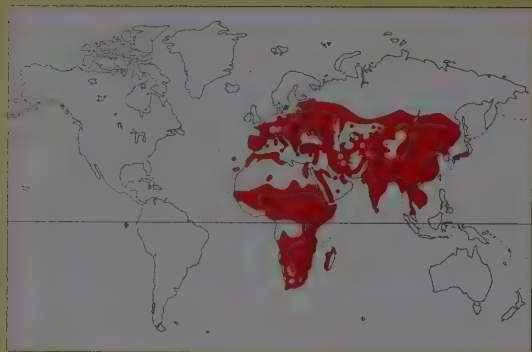
**Breeding.** Season thought to start mid-Sept in Comoros, Nov-Dec in Madagascar. Presumed to be monogamous. Nest in tree hollow, with eggs laid directly on to wood substrate within cavity. Normally 4-5 eggs, whitish and slightly tinted beige-green, average 45 x 38 mm; incubation by female, starting with first egg, period c. 20 days; nestlings

covered with white down; fledging c. 30 days.

**Movements.** Probably largely sedentary. Outside breeding season, some birds make erratic movements to areas where species not normally recorded.

**Status and Conservation.** Not globally threatened. Widespread in suitable habitat, although in some areas patchily distributed and distinctly uncommon. In Madagascar, reported to be possibly easier to observe in dry forest in W part of island, e.g. at Zombitse-Vohibasia National Park and Ampijoroa Forest Station, but whether because more numerous there is uncertain. Major threat is continued destruction of natural forest habitats, in both Madagascar and Comoros. Race *gracilis*, sometimes considered a distinct species, estimated to number only c. 100 pairs; research required. **Bibliography.** Andrianarimisa (1993), Appert (1968a, 1972), Benson (1960, 1981, 1985a), Benson *et al.* (1976-1977), Burton (1984), Cracraft (1971, 1981), Dee (1986), Delacour (1932a, 1932b, 1932c), Dresser (1895), Eguchi *et al.* (1993), Forbes (1880), Forbes-Watson (1967, 1969), Forshaw & Cooper (1993), Goodman & Putnam (1996), Goodman, Langrand & Razafimahaimodison (1994), Goodman, Pidgeon *et al.* (1997), Green & Sussman (1990), Hawkins & Wilmé (1996), Hawkins *et al.* (1998), Herremans & Louette (1992), Koenig (1984), Korzun (1988), Langrand (1995a, 1995c), Langrand & Goodman (1997), Langrand & Wilmé (1997), Lavauden (1929), Louette (1988a, 1988b), Lowe (1948), Maurer (1978), Maurer & Raikow (1981), Milon *et al.* (1973), Morris & Hawkins (1998), Nelson & Horning (1993), Nicoll & Langrand (1989), Rand (1936), Rasoloarison *et al.* (1995), Rued (1970), Safford & Duckworth (1990), Salvan (1970), Selater (1865), Sibley & Ahlquist (1990), Sibley *et al.* (1988), Sinclair & Langrand (1998), van Someren (1947), Stevens *et al.* (1995), Thompson (1987), Thompson & Evans (1991), Verheyen (1955a, 1955b, 1955c), Wilmé (1996).

Class AVES  
 Order CORACIIFORMES  
 Suborder BUCEROTES  
**Family UPUPIDAE (HOOPOE)**



- Medium-sized birds with long, thin, decurved bill, prominent erectile crest, broad rounded wings, and short but powerful legs.
- 26-32 cm.

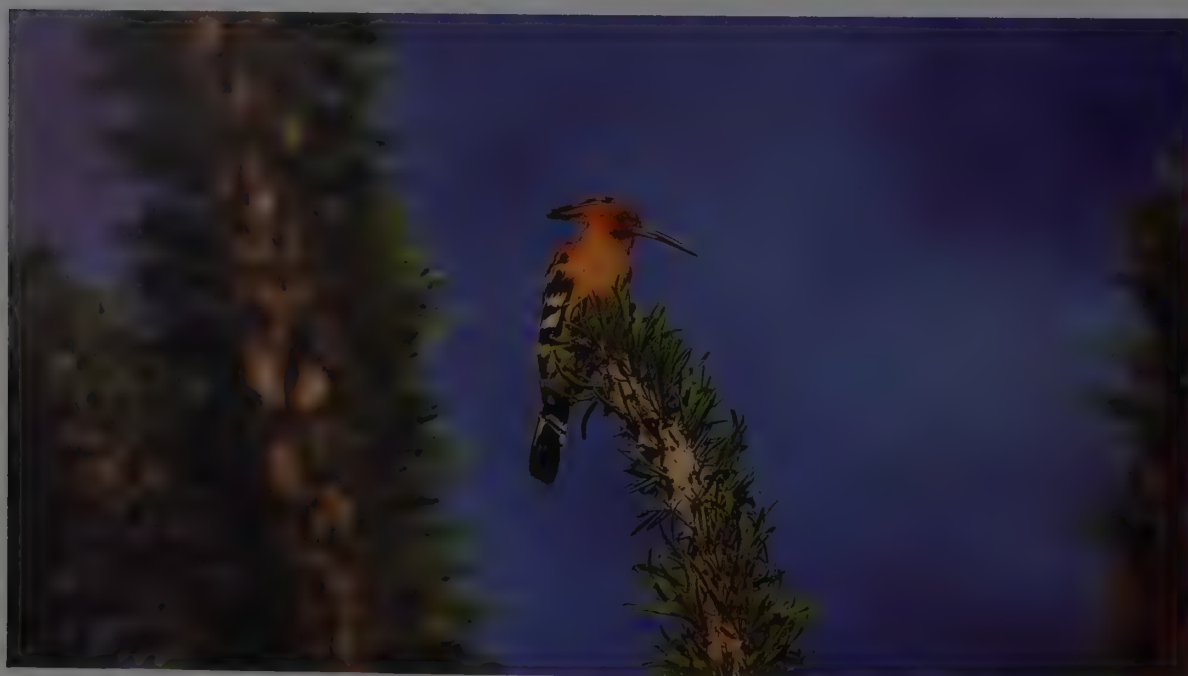


- Palearctic, Afrotropical and Oriental Regions.
- Open country with patches of bare earth or short grass; needs trees, walls or buildings with cavities.
- 1 genus, 1 species, 9 taxa.
- No species threatened; probably 1 extinct since 1600.

### Systematics

The Hoopoe (*Upupa epops*) is a highly individual species representing an equally distinctive family of Old World coraciiform birds. It has no particularly close relatives, but there is now fairly wide agreement on its systematic position. The Coraciiformes are loosely defined by a suite of characters which the Hoopoe partly shares, but at least two characters set it aside from the others. It is the only member of the order that lacks an expansor secundarium muscle, and it is also the only one in which the young are not gymnopaedic, being instead covered with down at hatching. It has ten primaries and ten rectrices, and there is no metallic gloss to the feathers. In addition, it has a tufted oil-gland which, in brooding females, produces an oil the smell of which repels intruders. Some authors consider these differences sufficient reason for the Upupidae to be placed in its own order, the Upupiformes.

Although it was at one stage believed to be related to the larks (Alaudidae), on the basis of extensive tarsal scutellation, or to the cuckoos (Cuculidae), the Hoopoe has long been regarded as linked to the hornbills (Bucerotidae). This is supported, in the first instance, through the Tertiary fossil *Cryptornis antiquus*, discovered in gypsum deposits near Paris. While the Hoopoe does, indeed, show a resemblance to the small hornbills of the genus *Tockus*, there is now general agreement that its closest relatives are in fact the woodhoopoes and scimitarbills (Phoeniculidae). These share with it a range of characters, both external, such as feather structure, pterylosis and bill morphology, and internal, including tongue structure, egg-white proteins and such skeletal features as bony stapes. Recent experiments in DNA-DNA hybridization have suggested that the Hoopoe diverged from the hornbills, and that the woodhoopoes and scimitarbills arose in turn from the Hoopoe.



There have been several proposals that the Hoopoe be split into three or more separate species.

Although the plumage differences do not seem particularly significant, the race living in Madagascar does have a distinct advertising call.

The male's resonant rolling phrase, repeated at short intervals, is quite unlike the familiar "hooping" call of other populations, and this has led many authors to treat the Madagascan form as a full species. On the other hand, males in other parts of the species' range have a similar rolling call, but they use this in courtship feeding or when feeding nestlings.

[*Upupa epops marginata*, near Ifaty, Madagascar.  
 Photo: Joe Tobias]



With its sandy to cinnamon or rufous-buff plumage marked with black and white, its striking fan-like crest and its long and slightly decurved bill, the Hoopoe is unlikely to be mistaken for any other bird, whether seen in the open country which it favours or in a more closed and confined habitat. It is equally distinctive in the air, when the markedly broad and rounded wings are flapped a few times and then briefly closed, producing a rather weak-looking, undulating flight that appears unsteady and irresolute, the bird at times resembling a gigantic butterfly. Despite this, the Hoopoe is capable of strong flight when necessary, as when in pursuit of aerial prey, and it is able to manoeuvre with surprising agility. As seen here, the nest is typically in a natural hollow, often in a tree.

[*Upupa epops epops*,  
Velada, Toledo, Spain.  
Photo: Miguel Angel  
de la Cruz]



There are three or four proposed arrangements of taxa within the Upupidae. The longest-standing viewpoint, adopted in all comprehensive handbooks and guides dealing with Palearctic, Afrotropical and Oriental avifaunas, treats the Hoopoe as a single polytypic species with nine subspecies. These range from western Europe south to South Africa and Madagascar, and east all the way to the Russian Far East, in the north, and the northern Malay Peninsula and Indochina, in the south.

Since the late 1980's and early 1990's, however, this all-inclusive judgement has started to lose ground in the general trend among taxonomists towards establishing narrower species limits in ornithology. The simplest and, perhaps, the most plausible revision, to be found mainly in regional works and articles on Madagascan birds but viewed sympathetically by broader authorities, including C. H. Fry and others in 1988 and R. J. Dowsett and F. Dowsett-Lemaire in 1993, involves the separation of the Madagascan population of the Hoopoe as a full species, *Upupa marginata*. This is based on the very distinctive advertising call of *marginata*, a form which is, furthermore, larger than its closest continental relatives and which may, as shown by C. W. Benson and colleagues, have an Oriental origin rather than a Palearctic or African one. On the other hand, the morphological differences between Madagascan birds and those in the rest of the species' range appear to be relatively minor, and it would be preferable to seek more evidence before a formal decision is taken to split *marginata*.

A more controversial interpretation is that adopted by C. G. Sibley and B. L. Monroe in their 1990 treatment of the taxonomy and distribution of the world's birds. They separate sub-Saharan populations, including that of Madagascar, as *U. africana*, the "African Hoopoe", arguing that, although sympatry between Palearctic populations and *africana* may represent merely a migratory overlap, the two forms are best regarded as distinct, allopatric species forming a superspecies. The problem with this assessment is that, with the exception of Madagascan birds, vocal differences between the two proposed species are negligible or non-existent.

Meanwhile, a yet more radical approach has been developed by R. Liversidge. On the basis of an examination of over a thousand museum skins, in combination with some field data, he proposes that the Hoopoe be split into four distinct species. These are the widespread Palearctic and Oriental *Upupa epops*, the essentially Sahelian *U. senegalensis*, the subequatorial *U. africana* and the Malagasy *U. marginata*. In this arrangement, it is simply the wing and tail patterns, along with song and flight behaviour, that are held up as both diagnostic characters and adequate isolating mechanisms. Engaging as this view is, it will doubtless require formal consideration before being adopted or rejected. One current stumbling block involves determining the most appropriate attribution of the subspecies *major* and *waibeli*: the former occurs north of *senegalensis*, and the latter is disjunctly interposed between *senegalensis* and *africana*. In the absence of biochemical analyses of taxa in the genus *Upupa* and of behavioural tests on reactions to vocalizations, especially mutual responses between nominate *epops* and *marginata*, it seems safer at present to treat them all as conspecific.

There was, however, at least one other member of the family. A large, probably flightless or near-flightless hoopoe, *Upupa antaios*, is known as a fossil from the island of St Helena, in the South Atlantic Ocean, some 1700 km west of the nearest point of the African continent. It probably became extinct only after the island's discovery by early European voyagers, who brought with them a variety of mammals, notably cats, which would have caused the rapid extinction of many endemic birds within as short a period as 40 years.

Even if one accepts that the bird on St Helena was a separate species, and that the one on Madagascar probably is, and, indeed, even if it is eventually decided that *Upupa epops* as currently constituted should be split into four species, all forms should remain united as a superspecies. None of the populations overlap, except where migrants and residents converge. There would seem little doubt that, in this respect, the Hoopoe represents one of the most remarkable instances of homogeneity within any avian family, and a startling example of specialization for the successful exploita-



Dusting, to rid the plumage of excess preen oil and probably also of any unwanted parasites, may be a substitute for bathing in water, for it occurs mostly among those birds, such as the Hoopoe, which live in open areas with bare soil or sand, and where water, if available at all, is generally scarce. The bird often creates a shallow scrape in the ground, and then adopts a sitting posture; with wings drooping and feathers fluffed, it tosses sand or dust on to its plumage and shakes this through the feathers, periodically turning around or shuffling forwards. A classic procedure of the Hoopoe is to rake up sand or earth around its breast with the bill, using its legs to toss dust up into the plumage.

[*Upupa epops epops*,  
Raimat, Lleida, Spain.  
Photo: Jordi Bas Casas]

tion of a huge ecological niche. This feeding niche is represented in the main by the insect fauna, mostly in the form of larvae, to be found just below the surface in the soils of the drier regions of the Old World, although the degree of flexibility that the birds have in exploiting surface-dwelling animals (see Food and Feeding) is perhaps the crucial factor in the species' success in remaining a single, polytypic entity. The Hoopoe's range covers a vast area, from the Gulf of Finland in the north to as far as Cape Town in the south, and from Senegal in the west to the Lower Amur River in the east, albeit with breaks for deserts, forest and high mountains. There are few, if any, other bird species that can be found with such continuity of distribution.

### Morphological Aspects

A medium-sized bird, the Hoopoe is immediately recognizable on account of several highly distinctive features. These are the striking fan-like erectile crest, the distinctive long, thin and slightly decurved bill, the bold black-and-white wing and tail patterns, the curious bounding flight, and, except in Madagascar (see Voice), the highly characteristic spring song. Of the total body length of 26-32 cm, the bill constitutes 5-6 cm and the tail 8-10 cm. Body weight varies greatly both seasonally and regionally, ranging from 47 g to about 90 g, but with little difference between the sexes. The wings are broad and rounded, with a span of 42-46 cm. They are strongly patterned white on black, with up to five broad bands extending across the secondaries and greater coverts, and in some subspecies a further white band crossing both the primaries and the secondaries subperipherally, the fawn-coloured lesser coverts producing a broad inner leading edge. As is to be expected, the wings are rather longer in the long-distance migratory forms *epops* and *saturata* than they are in the more sedentary ones, such as *major* and *senegalensis* in Africa and *ceylonensis* and *longirostris* in Asia. The black of the secondaries extends across the back, as do one or more of the white, often sandy-stained, secondary bands, and there is a small white patch on the rump. The tail is moderately broad and square-ended, and is black, with a broad inverted white chevron crossing it more or less centrally.

Not only is the plumage pattern distinctive, but the flight is equally so. The Hoopoe flies with an erratic butterfly-like flapping, the wings being briefly part-closed after each very rapid

beat or each short rapid burst of beats, resulting in a strongly undulating pattern. At times, the flight also recalls that of a Northern Lapwing (*Vanellus vanellus*), with rapid, looping climbs and long, wavering plummets. Although it can sometimes appear weak and indecisive, the Hoopoe's flight is in fact strong: the shape of the wing bestows considerable speed and manoeuvrability when the bird pursues prey in the air.

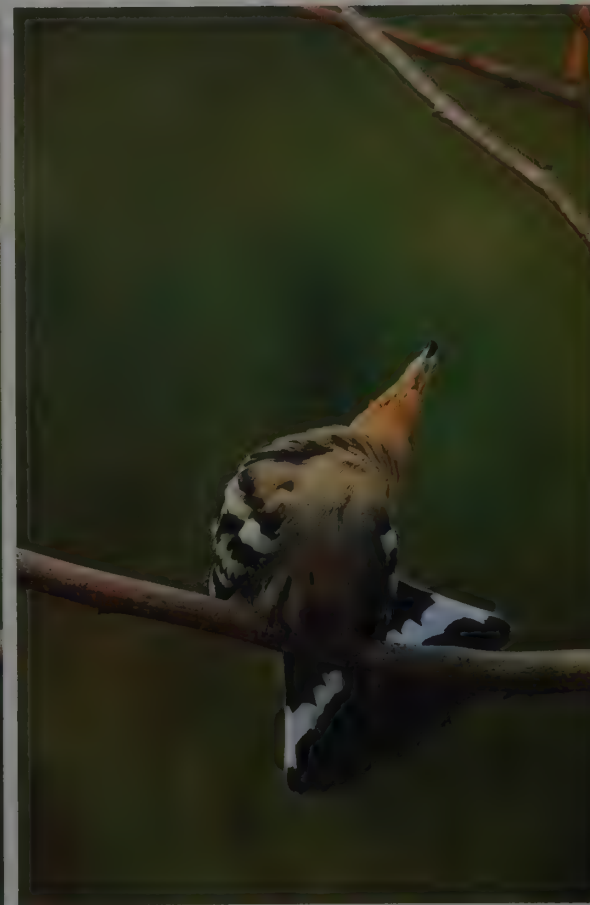
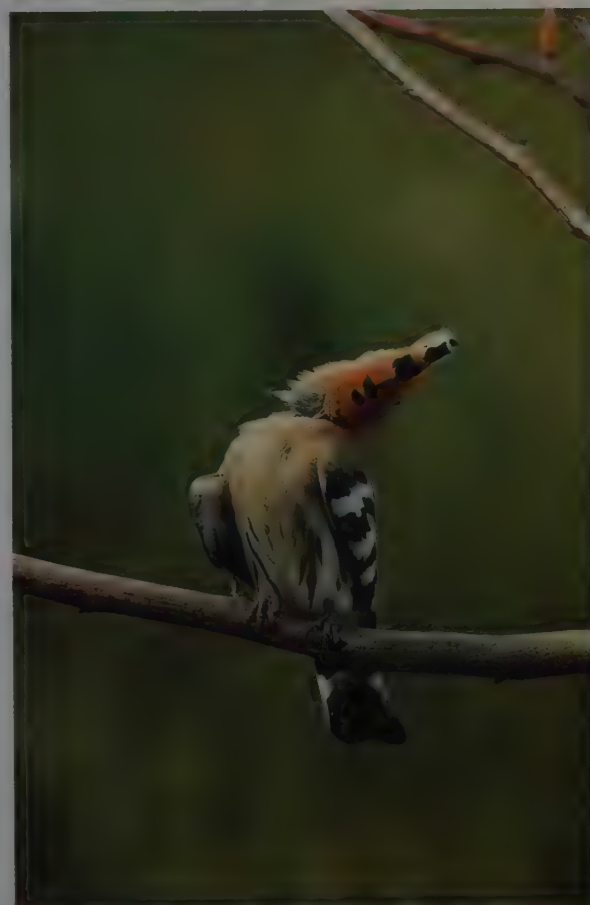
The bill, black with a pinkish-fawn base, is long, thin and tapering, delicately decurved and strongly compressed laterally. These morphological features are distinctive adaptations for foraging in the ground for soil-dwelling insects, the slight curve of the bill maximizing the efficiency of the probing force from the muscles in the bird's often broad-looking neck. Moreover, the skull and jaw musculature is highly modified, enabling the bill to be opened during probing. The tongue is characteristically reduced. It is worth noting that food items are typically no longer than the length of the bill (see Food and Feeding).

The blackish legs are rather short, with a tarsus length of 20-26 mm, reflecting the species' adaptation to ground-feeding on dry, open substrates that are bare or have only a very short herb layer. Although the feet have been described as rather weak, they serve to support the bird when it clings to the vertical surfaces in which its nests are built. The three forward-pointing toes show a slight tendency to fuse at the plantar surfaces, with the middle and outer toes united at the basal joint, this being a typical coraciiform feature and one which may allow greater purchase at the rim of the nest-hole; the first toe is as long as the others. While characteristic feeding movements involve short steps and shuffles as the bird focuses on investigating patches of ground, the gait is well developed, with strong walking and short runs as necessary. The Hoopoe perches freely in trees and on buildings.

A particularly striking feature of the Hoopoe is its prominent crest. This is fawn, concolorous with the head, and has broad black tips. In some subspecies, the middle and rear feathers of the crest have whitish subterminal bars or, as in Madagascan birds, white extreme tips. The crest forms a remarkable full fan shape when erected, falling to a blunt elongate point behind the head when compressed. It is momentarily fanned whenever the bird settles after a short flight, and is similarly extended at the least excitement.

The body plumage is generally of a fawn, or rufous-buff, colour. This varies geographically, however, from warm sandy-





Since it appears not to bathe in water, the Hoopoe not only dust-bathes rather frequently but also needs to preen at regular intervals in order to maintain its feathers in good condition. Preening involves both nibbling of the feathers, with the mandibles open, and stroking them, with the bill closed as it is drawn down over the feathers.

The head has to be attended to by scratching, in the case of the Hoopoe by direct scratching. For a species which feeds chiefly by probing in soil, it is also important that the bill and feet be regularly cleaned of dirt and other extraneous matter, especially during the breeding season when the bird may need to maximize its foraging efficiency in order to provision its mate and young in the nest.

To achieve this, the Hoopoe constantly picks dirt from its feet, and often wipes the bill on a branch or similar object. Sunning, in a posture previously thought to be adopted as an anti-raptor response, is another type of comfort behaviour indulged in by the Hoopoe, but, for a bird that can often be so conspicuous, there seems to be surprisingly little known about these aspects of its life.

A striking feature of the Hoopoe, and one that is shown particularly well in these photographs, is the very broad and rounded black tail with a wide white band across its centre.

[*Upupa epops epops*,  
Raimat, Lleida, Spain.  
Photo: Jordi Bas Casas]



Although the Hoopoe's characteristic song in spring is delivered most often from an elevated perch, such as a rooftop or high in a tree, it may at times be given from the ground or even, more occasionally, in flight. The singing male inclines his head downwards, apparently in order to increase the volume of air in the vocal passages; the neck is inflated, and with each note emitted the throat pulses outwards. This is perfectly demonstrated by this individual. The song can be heard for several weeks prior to egg-laying. Over the species' huge range there appears to be little variation in this vocalization except in Madagascar, where Hoopoes utter a purring song.

[*Upupa epops epops*, Andalusia, Spain.  
Photo: Rolf Kunz]

buff through pinkish and cinnamon to pale chestnut. Northern Hoopoes and those inhabiting dry, desertic regions tend to be paler, while those living in areas of higher rainfall and nearer the equator have a more saturated coloration. In general, the head, crest and mantle are somewhat more intensely coloured than are the underparts, and the crest in particular always appears to be the most strongly tinted. The sexes are much the same in size and appearance, males usually being slightly larger; the female of the subspecies *africana* shows greyish-rufous lesser coverts. Both adults and juveniles have a brown iris, whereas that of nestlings is bluish-black.

Adult Hoopoes begin the annual post-breeding moult mainly in the breeding area, from July or August in the Palearctic Region. The first feathers to be replaced are those of the head, including the crest and throat, and those of the mantle and chest, occasionally followed by a few inner primaries or some tail feathers. The moult is then suspended during migration, recommencing with the shedding of the wing and tail feathers, usually in the winter quarters. The tail moult starts at the same time as that of the primaries, and begins with the central pair of rectrices, but the subsequent sequence is apparently irregular. The secondaries are moulted ascendantly and descendantly, from the longest of the innermost feathers (S7), beginning at the same time as the first primary (P1) is lost. It is not known whether any pre-breeding moult occurs.

Juveniles, in their drab version of the female plumage, usually do not start moulting until they have reached the winter quarters, although individuals which fledge early in the season replace many of the head, neck, chest and some other feathers from August, while in the breeding area. After their first moult, they immediately acquire the colour and pattern of the adults.

## Habitat

Throughout the breeding range, Hoopoes require two basic habitat elements. These are bare or short-grass open land on which to feed, and vertical or near-vertical cavity-bearing features in which to nest. As a consequence, they occur most frequently in farmland, especially where old walls and ruined outbuildings provide crevices, and in tree-bordered pastures, parkland, orchards,

sand-heathland, olive groves, vineyards, wooded steppes and savannas. They are sometimes found even in treeless, unfarmed areas if there are low cliffs and dry banks in which to nest. Trees are commonly used for cover when the birds are disturbed.

Since Hoopoes require food that is of a particular size class and, doubtless, of reasonable abundance, the species shows a strong propensity for warmer and, at least seasonally, drier regions. The Afrotropical subspecies favour a variety of types of grassland, chiefly *Acacia* savannas, in which the density of trees appears immaterial, so that they therefore penetrate the forest-savanna mosaic; they also visit well-watered lawns, and farmsteads with sweetgrass (*Cynodon dactylon*). In North Africa and southern Europe, Hoopoes are relatively abundant in landscapes modified from Mediterranean dry woodland to orchards, olive groves, vineyards and pastures, and in the Canary Islands they are most frequent in semi-desert habitats. In its wide range across central Asia, the species is found in steppeland and the open parts of mixed forest-steppe areas, on sparsely vegetated plains, in valleys and foothills with cliffs, and in glades and clearings in wooded tracts. In South-east Asia, these birds also use open, sandy ground below strand vegetation, and coastal dune scrub, as well as fields and the margins of rubber plantations, in Malaysia more or less exclusively at plains level. Only in Madagascar, where the species is commonest in heavily wooded forest margins, is it known to penetrate primary deciduous forest.

Although Hoopoes may, in traditionally farmed areas, reach higher densities in the neighbourhood of villages and habitations than they do in surrounding landscapes, this depends on nest-site opportunities. Moreover, they avoid high-intensity farmland and intensively managed agriculture, systems found mainly in western Europe and South-east Asia. They also tend to avoid areas with damp substrates, such as wetlands, reedbeds, large tracts of closed woodland and forest, and areas with high precipitation. This last factor may explain why, at least in the western half of their huge range, they are rarely found in mountains, preferring mostly lowland and hilly breeding habitats from sea-level to a maximum of 1500 m in Europe, Africa and Madagascar. In Afghanistan and Pakistan they generally keep below 2000 m, but sometimes stray above 3000 m. In the Tibetan part of the Himalayas, Hoopoes have been found breeding as high as 2800 m, and on migration they have been recorded at even greater



Hoopoes are commonly seen probing in the ground for food.

The typical foraging method is to walk about in areas of short vegetation, repeatedly jabbing the long bill at different angles into the substrate to test it, now and again stopping to insert the bill up to its full length. On detecting an object beneath the surface, the bird assesses its suitability as food by slightly opening and then quickly closing the tips of the mandibles; edible items are drawn out in the bill tip; the crest is usually held flat during the process. Hoopoes also forage by poking about among leaf litter, rubbish and animal droppings, and the bill is also used to turn over heavy objects such as stones.

{*Upupa epops africana*, Lake Nakuru National Park, Kenya.

Photo: Dave Richards]



altitudes, at about 6400 m in the Mount Everest area in September and at around 5790 m in Nepal in May.

### General Habits

Hoopoes are never very gregarious, always breeding solitarily and in territorial pairs, and also feeding singly or in pairs. Small, loose flocks of up to 25 individuals do sometimes occur outside the breeding season, on migration, and small feeding flocks of fewer than ten birds are sometimes encountered in the pre-breeding or post-breeding periods.

The Hoopoe is a relatively tame bird, and its use of inhabited or utilized buildings in which to nest reflects its confiding nature, although it can also be highly discreet and shy in areas where it is persecuted (see Status and Conservation). The extraordinary crest conveys the bird's rapidly shifting "mood", being held closed when the bird is relaxed, and fanned when it is excited or alarmed. The evolution of the crest as a signalling device in so weakly sociable a species deserves study, particularly as no other avian species has developed such an ornament to an equivalent degree. The same might be said for the striking black-and-white elements of the plumage. It may well be that these morphological features are as important as signals to potential predators as they are to conspecifics. Away from the nest, there appear to be few records of Hoopoes being taken by predators, except where they fall victim to Eleonora's and Sooty Falcons (*Falco eleonora* and *F. concolor*), which catch them in flight as they move south over the sea on autumn migration. It is possible that the strong patterns have an aposematic function, warning of some distastefulness in their flesh.

Like the other Coraciiformes, the Hoopoe is a diurnal bird. At the onset of darkness it goes to roost, usually solitarily or in pairs, mostly in trees, but more rarely in holes. Cliffs are sometimes used as roost-sites in areas with scanty trees, as also are small buildings in traditionally farmed areas. Roosting sites can be quite exposed, and some individuals will return to the same perch for weeks at a time, even if disturbed. Roosting places are often close to the trunk. In Egypt, Hoopoes were found roosting 1-2 m up on stems of banana trees, clinging to the trunks in the manner of woodpeckers (Picidae). When tending nestlings, the

female typically roosts in the hole with them, while the male sleeps elsewhere, as far as 700 m from the nest.

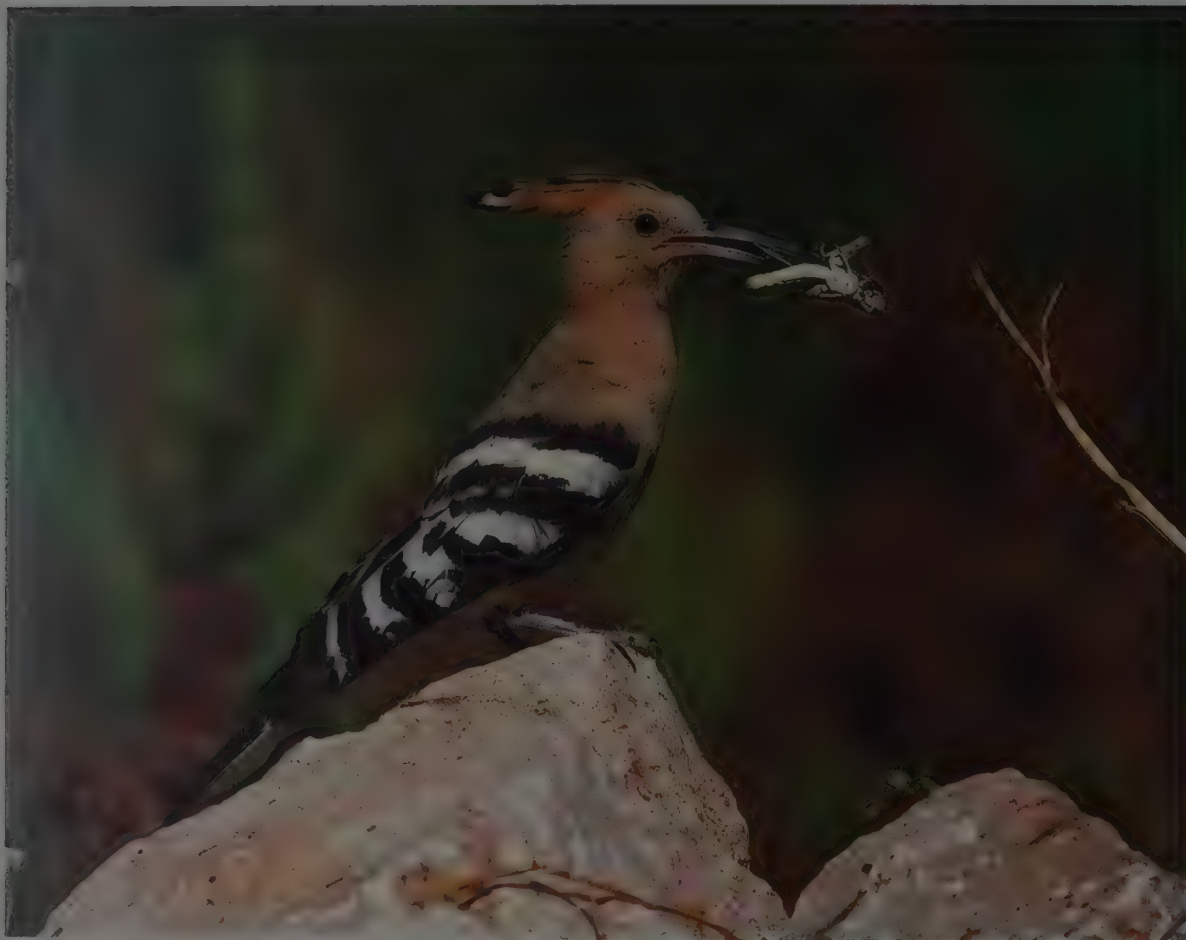
A particularly typical and well-known response of the Hoopoe in the presence of ground predators and humans is to freeze, remaining quite motionless, so that it stands a better chance of escaping detection. When perched on a branch, it will also, like the trogons (Trogonidae), turn its back to the intruder, again becoming surprisingly inconspicuous in spite of the bold pattern of the upperparts. The anti-predator responses of the female and her chicks at the nest are particularly distinctive and highly evolved (see Breeding).

It has frequently been reported that an adult Hoopoe, when surprised out in the open and away from cover, can respond to the sudden appearance overhead of a bird of prey by flattening itself against the ground, with wings and tail spread wide, the head thrown back and the bill pointing upwards, so that its outline is lost and it becomes virtually invisible. This behaviour appears to begin and end rather abruptly, which would support the notion that it is an anti-predator response. An alternative interpretation, however, and one which is, as Fry and colleagues have argued, more likely, is that the spreadeagle posture is that adopted for sun-bathing. This explanation does seem to be very probable, especially since the members of another coraciiform family, the bee-eaters (Meropidae), are known to assume an almost identical posture for sunning, again starting and finishing suddenly.

There is otherwise surprisingly little information on the comfort behaviour of the Hoopoe. This species is reputed not to bathe in water, but it certainly dust-bathes rather frequently.

### Voice

The names "Hoopoe" and "*Upupa*" both reflect the distinctive spring advertisement song of the male. This is a beautiful, mellow, resonant, hooting phrase, "hoop-hoop-hoop", one of the most evocative and typical sounds of spring mornings in the countryside of the Mediterranean countries and elsewhere. Each phrase consists of two, three, four or five notes, and the phrases are commonly given with short pauses of up to about one second between them. Phrases can be grouped together, into "sentences",



Insects provide the main source of food for a great many bird species. The Hoopoe consumes a considerable number of ground-dwelling insect larvae and pupae, but it also takes many adult insects, among them crickets and grasshoppers, as well as those, such as beetles, which have hard elytra. Field observations suggest that Hoopoes prefer larger insects, those with a body more or less as long as the bird's bill. These relatively sizeable prey, before being swallowed, are usually beaten on a hard surface in order to remove the legs and wings and other indigestible parts.

[*Upupa epops epops*, Ayranci, near Eregli marshes, Turkey. Photo: Axel Halley]

which themselves are separated by slightly longer pauses of several seconds' duration. The song is very similar to that of the Himalayan Cuckoo (*Cuculus saturatus*) and that of the African Cuckoo (*Cuculus gularis*), but the cuckoos' songs are usually distinguishable by their having four notes, as against the Hoopoe's somewhat more customary three or two notes.

Some male Hoopoes, however, utter phrases with four or five notes, and phrase length seems also to play a role in breeding success. In studies in southern Spain, M. Martín-Vivaldi and colleagues have shown that female Hoopoes, in the early spring, are attracted preferentially to songs with long phrases, and that females paired with males singing long phrases are more successful. Such females not only laid earlier and produced larger clutches than did females paired with males singing short phrases, but also more frequently attempted second broods. Moreover, males with long song phrases were more efficient feeders, bringing more food for the brood, so that a greater number of fledglings was reared both from their first clutches and through the entire season. The relationship between high breeding success and the length of the male's song phrases was not the result of age differences among individuals.

The song is usually delivered from a perch in the upper part of a tree, or from a rooftop. It is uttered with great persistence, the overall rate often reaching a total of 20-30 notes per minute, and the song extending over many minutes at a time. When delivering this song, the male inclines its head downwards; this is apparently done in order to increase the volume of air in the vocal passages, since the neck is inflated and the throat pulses outwards with each note. The song period lasts from several weeks before the commencement of breeding activities until about the time when the clutch is laid.

Other vocalizations involve no inflation of the neck and no resonance, and are uniformly raucous. The most frequently heard is a "Long-caw", given in disputes with conspecifics and in courtship, and consisting of a harsh rasp, "schrää". A "Short-caw" is

given by the male when showing a prospective nest-site to the female and as a preliminary to copulation. Both of these, which are sometimes referred to as "swizzle" calls, are sometimes accompanied by an occasional rattling call, a quiet "tr", which presumably conveys excitement. When the male proffers food to either his mate or one of his offspring, he utters a feeding call that consists of a rolling chirp, which could be transcribed as, for example, "gurr". When the female and young are disturbed in the nest-hole, they produce a snake-like hiss. The food-begging call of newly hatched nestlings is a faint high squeaking, but this becomes a louder "sisisisi" as they get older, and is given in response to an approaching adult. After fledging, it becomes a thin, whistling "czririri czririri".

While this short summary of the Hoopoe's voice is applicable throughout almost all of its range, there is a notable difference in Madagascar. There, the male's song has transmuted into a soft, resonant, rolling purr, "rrrrràààòoooo", lasting about one second and repeated at regular brief intervals. This is apparently closer to the feeding call of the nominate subspecies.

### Food and Feeding

The diet of the Hoopoe consists almost entirely of animal food, very occasionally supplemented by small seeds, berries, leaves, stems and rhizomes. This is a mostly insectivorous species, its long, slightly decurved bill being adapted for sensing and extracting mainly the ground-living larvae and pupae of insects. It forages solitarily, with the crest feathers generally depressed but sometimes raised. Typical foraging places are bare ground or short-grass areas with scattered tracts or patches of longer herbs, where it investigates recently or chronically disturbed earth, as for example along tracks, by roadsides, among vines and under trees where the ground vegetation has been eliminated by a combination of shade, grazing and trampling.



Hoopoes walk about, testing the ground with constant short jabs of the bill at varying angles. From time to time they pause to insert the full length of the bill into soft or hard substrates, opening and closing it to assess and, if appropriate, to seize objects that are sensed, presumably, with the bill tip. It appears that they detect the holes of mole-cricket (*Gryllotalpa*) and cockchafer larvae (*Melolontha*) by sight. When they dig vigorously, making the soil fly in their bid to improve downward access, it is probably in pursuit of prey that are capable of burrowing or retreating backwards. The pressure of the bill combined with movement by the bird creates a wider funnel-shaped hole, facilitating prey extraction. In addition to digging, however, Hoopoes also probe into and flick over leaf litter and dry animal droppings, and they will poke about among rubbish at dumps and at fly-blown carrion. The bill is also utilized as a lever to displace stones and heavy objects. More rarely, it is used to flake off bark in order to extract various larvae and pupae of insects, and the species has been seen foraging among lichens on tree boughs and old stonework.

The Hoopoe is well adapted also for feeding on hard sclerotized insects such as adult cockchafers, as well as mole-cricket, ground-cricket (*Gryllidae*) and stag beetles (*Lucanidae*). Indeed, such insects, with a body size preferably up to the length of the bird's bill, are often favoured. Larger adult prey are beaten on the ground, the bird sometimes flying with them to a particular favoured site to hammer and process the prey, which normally involves removing the indigestible legs, elytra and wings. Lizards are also beaten, the bill sometimes puncturing the head, while the detached tail is readily caught, tossed into position and swallowed. While larvae and pupae may be taken lengthwise into the bill and swallowed direct, mobile adult prey items are generally held transversely in the bill tip, and are normally consumed with a quick upward jerk of the open bill to align them with the tongue. Prey are carried in a similar crosswise position during courtship, and for transportation to the nestlings.

Apart from crickets and mole-cricket, the staple insect food of the Hoopoe consists of beetles and their larvae, and the caterpillars and pupae of moths, as well as locusts and grasshoppers, bugs, cicadas, ant-lion (*Myrmeleonidae*) larvae, earwigs (*Dermaptera*) and ants. Among the commonly taken beetles are

those of the families Scarabaeidae, Geotrupidae, Carabidae, Elateridae and Chrysomelidae. Moth prey include members of the families Noctuidae, Sphingidae, Geometridae, and others, notably the pupae of the Pine Processionary Moth (*Thaumetopoea pityocampa*), a serious pest in the forest areas in which it occurs (see Relationship with Man). Other invertebrates consumed include spiders, centipedes, millipedes, woodlice, snails and slugs, but relatively few earthworms are eaten, this doubtless being due to the usually dry condition of the substrate. Hoopoes are able to exploit local abundances, so that the food-species spectrum is highly variable with context, and can be relatively narrow in any particular habitat. Swarms or outbreaks of relatively slow-flying insects, such as cockchafers, termites and some Diptera, can even induce these birds to indulge in aerial foraging.

The body size of prey varies generally from 10 mm to 150 mm, but prey items 20-30 mm in length, such as crickets and cockchafers, are preferred. Large food items such as stag beetles may be delivered to chicks which, at six days old, are no more than three times bigger than the prey item itself. In the majority of cases, however, the foods brought to nestlings consist of softer-bodied animals. In one study in Germany, 56% of all items delivered, and 97% of all items identified, consisted of lepidopteran or coleopteran larvae, and even at 14 days the young were still being fed 90% insect larvae.

Larger and harder food items have to be broken up before being presented to the young. Traditional hammering places are often used, and these are usually no more than 50 m from the nest-site. Typically, an area of ground 0.25 m<sup>2</sup> in extent serves for this purpose, and there the indigestible or sharp body parts are removed from prey items.

Food is gathered relatively evenly over the daylight hours, but chiefly in the early morning and early evening, and feeding bouts usually last one or two hours. During the breeding period, foraging is generally carried out within some 300 m of the nest-site, although this activity can, on rare occasions, occur at up to 2 km from it.

Only rarely do Hoopoes regurgitate pellets, these measuring 8-10 × 12-20 mm. For the most part, they void arthropod chitin with the faeces. Their droppings are hard and stone-like in appearance after a few days.

Although first and foremost an insectivore, the Hoopoe not infrequently captures vertebrates, primarily lizards, which are often comparatively abundant in the open, sunny habitats preferred by this species. Such prey have first to be immobilized, and they may be carried to a particular favoured site for processing. The bird beats the lizard on the ground, sometimes puncturing the reptile's head with its bill; the tail, which quickly becomes detached, is easily caught, and is tossed up and swallowed. Besides animal food, Hoopoes consume a very small amount of vegetable matter in the form of berries and seeds, but these seem to make up a minimal proportion of their diet.

[*Upupa epops epops*,  
île de Ré, France.  
Photo: Thierry Moreau/  
Bios]





It appears that the Hoopoe seldom, if ever, drinks. It is able to obtain all its moisture requirements from its almost exclusively invertebrate food.

### Breeding

Hoopoes form monogamous pair-bonds, but even among resident populations it appears that the bond lasts only for one season. On the other hand, the nest-site is commonly traditional and is used from year to year; in one exceptional case, a site was occupied for 17 years without a break. An interesting observation in central Europe concerned a nest-hole that was used for two successive broods in the same season, by two different females. Unfortunately, it was not determined whether the same male was involved, but, if it was, this would illustrate just how rapidly divorce can occur in the species. In any case, the observation certainly demonstrates, as does the unbroken 17-year use of one hole, the extent to which the key resource for breeding is the nest-site.

The insistent, far-carrying territorial singing by males, especially early in the morning, proclaims an area in which this resource is present. When nest-sites are somewhat clumped, or when food resources encourage several pairs to stake claims on areas where nest-sites are few, the intensity of singing in the immediate pre-breeding period escalates dramatically, with long bouts and song-duels then being common. Sometimes fighting erupts and, as with other bird species, this very occasionally results in fatalities. Even when territorial neighbours have found their separate nest-sites, such singing can continue until the young have fledged.

There have been records of Hoopoes nesting very close together. Examples include pairs nesting on the same building, in the same garden and, once, with a shared entrance under adjoining roof joists. These exceptional cases, however, misrepresent the species' normal breeding dispersion, which varies with the quality and extent of the foraging substrate. In some more peripheral areas densities can be as low as one pair per 100 km<sup>2</sup>, but in central areas the birds are dispersed at between 20 and 60 pairs per 100 km<sup>2</sup>. In Germany, one study found seven pairs in 25 km<sup>2</sup>, this rising to ten pairs with the provision of nestboxes.

In central Europe, densities as high as eight to 15 pairs per 10 km<sup>2</sup> have been reported, and in southern Europe as many as 4.3-5.2 pairs per km<sup>2</sup>. These highly variable figures must surely reflect differences in absolute terms, indicating that feeding substrates in southern Europe hold a higher food biomass than do those farther north; at the same time, however, they seem likely to reflect also the greater continuity of feeding substrates in the south, as against an increasingly patchy distribution of suitable areas in the north. Home ranges, or foraging areas, in central and northern Europe are generally around 70 ha in extent, but some may cover as few as 35 ha in good-quality Palearctic habitats, as has been recorded in Slovakia and also in Japan, and evidently under 20 ha in parts of the Mediterranean Basin. Where nests are very close together, the foraging areas are likely to be in largely opposite directions. The level of hostility of resident pairs towards intruders into these foraging areas is, however, unclear, though it is apparently very limited. Hoopoes seem to be willing to travel up to 2 km from the nest to regular feeding areas.

Singing is the principal self-advertisement display of the male Hoopoe, and is the key dispersive mechanism among breeding pairs. In antagonistic behaviour, aerial and terrestrial chasing between males, as well as between females, has been recorded. During aerial chases, the birds fly in an excited manner back and forth, or continue the pursuit near the prospective nest tree, with the encounter then petering out as the participants return to the ground to compose themselves and take stock. Fighting between two males is said to be common and sometimes severe, the combatants leaping and fluttering in the air like gamecocks. An experiment with a stuffed Hoopoe caused both members of a pair to make pecking attacks with the open bill, sometimes simultaneously, emitting scolding, snoring sounds with the crest held raised.

Pair formation has been observed in South Africa while the birds were still in small pre-breeding groups. After the initial period of threatening and chasing other males, the males began chasing the females, but in a much less aggressive manner than before. Later, in the immediate pre-breeding period, when Hoopoes were still occasionally coming together in groups, courtship feeding began. Next, the males started to search for nest-sites, this resulting in the permanent break-up of the groups and the establishment of territories.

*Hoopoes always nest in a cavity, which is often a hollow among rocks or boulders in those open areas where suitable trees or other hole-bearing sites are scarce. The chicks are downy in their first three to five days of life, before the long feather quills break out from the sheaths. For the first two weeks or so they are brooded by the female, while the male provisions the family, but afterwards the young are fed by both parents. The nestlings' white gape-flanges provide a strong signal for the adults in the poorly lit interior of the nest-hole. Although the female attempts to remove droppings, faecal material soon builds up and the nest-hole often takes on a foul smell.*

[*Upupa epops epops*, Pinto, Madrid, Spain.  
Photo: Luis Miguel Ruiz Gordon]



By about the end of the second week, the young have already started to develop the conspicuous crest of the adults, and their wings show the characteristic strongly barred pattern of black and white. At this age they are capable of moving about in the nest.

By the end of the third week they sit at the entrance of the hole, awaiting the arrival of a parent with food, and a week or so later they are fully fledged.

The juvenile's bill is noticeably shorter and somewhat straighter than that of the adults, and will not reach its full length until several months after the young bird has fledged.

[*Upupa epops epops*,  
Madrigal de la Vera,  
Cáceres, Spain.  
Photo: Jorge Sierra]



Where the individuals are long-distance migrants, as in Europe, they usually arrive singly in the spring, males apparently ahead of females, with pair formation taking place only once the females arrive. The nest-site is sometimes chosen in the course of courtship, but usually soon after the pair-bond is first established. The male attracts the female to the site by moving excitedly in and out of the cavity and walking around and around outside it. Following the selection of the site, the pair-bond continues to be consolidated over about two weeks, during which copulation is regular. Courtship feeding is mainly a non-ritualized event: the male approaches the female with a food item held in the bill tip, and repeatedly gives the feeding call (see Voice) until the female takes the offering. Copulation follows this feeding: after a series of mock-feeds the birds pause, and then copulate, the male sometimes but not always extending his wings for balance, and cloacal contact lasting up to five seconds. Mating usually occurs on the ground, but sometimes on a large branch or stump, and frequently near the nest-site.

The breeding season varies with latitude. Laying starts in January in the Canary Islands, south Asia and Central and West Africa, but occurs from mid-February to the end of May in southern and central Europe and in central and eastern Asia, and from September to December in South Africa and Madagascar. In East Africa, the season covers the months from August to January.

The nest is situated in a hole in a tree or wall, in a crevice amid boulders or in an old building, or in a termite mound. Sometimes nestboxes are occupied, and in South-east Asia clumps of epiphytes are occasionally used. Sites up to 2 m from the ground are preferred, but they can, exceptionally, be as high as 12 m. Cavities are located and cleared by the male, the latter duty occasionally being shared by the female, but there is never any excavation from scratch. Little or no nest material is added, although the birds sometimes lay down a scant lining of grass, leaves, wool, feathers and rubbish.

As with season, clutch size also varies with latitude. As many as five to eight or even, exceptionally, twelve eggs are laid in the central and northern Palearctic, with only four to seven in the tropics and subtropics. There seems, however, to be a significantly smaller clutch size in the Southern Hemisphere, where ten clutches averaged 5.5 eggs, than in central Europe, with a mean of 6.9 for 62 clutches. The eggs are round-oval, smooth

and matt, and marked with conspicuous pores. They are of a very pale milky-blue colour when fresh, but soon turn a pale dirty greenish-grey, and are further discoloured by contact with the increasingly filthy nest interior. Egg sizes vary somewhat. The smallest were nine eggs from South Africa which averaged  $23.7 \times 16.9$  mm, whereas the mean size of 124 from central Europe and Asia was  $26 \times 18$  mm. The eggs, which weigh 3.4-4.4 g, are laid at daily intervals.

Only the female incubates, starting with the first egg, and she is fed mostly by the male. The chicks hatch asynchronously after a period of 15-18 days of incubation. They are downy in their first three to five days of life, but later they are covered in long spiny quills as the feather sheaths break out. By the fourteenth day, the crest is developing and the young are fairly mobile, giving defence reactions. Once they reach 20-24 days of age they customarily sit in the nest entrance, awaiting parental feeding visits. The nestling period is variable, but usually occupies 25-30 days. Often, one or more of the younger chicks in a brood develops slowly or starves. Well-nourished chicks grow from about 3.5 g at hatching to an adult weight of about 70-75 g by 20-26 days of age.

While the young are brooded by the female, up to the age of 9-14 days, the male has charge of feeding them, delivering items initially at a rate of five to eight times per hour. Later, both parents share the feeding duties, with an average of 14-6 visits per hour recorded when six 18-day-old chicks were in the nest. In one study, the chicks received 30-50 feeds per day in the early nestling period and 70-80 in the middle phase, this falling back to 40-50 in the final stages, although it is possible that prey sizes and weights increased throughout the period. The white gape-flanges of the young serve as a strong signal for the feeding parents in the weak light of the nest-hole.

The anti-predator responses of young Hoopoes and brooding females at the nest are extraordinarily well evolved. Both the female and her nestlings rapidly modify the uropygial gland to produce an evil-smelling fluid, with a stench like that of rotting meat. In young birds, this gland is active at four days and reaches its maximum size at twelve days, before being gradually reabsorbed as fledging approaches. In addition, however, nestlings are capable, from the sixth day, of directionally squirting copious amounts of liquid faeces and cloacal contents at an in-





In the final week or so before leaving the nest, the young Hoopoes become very active and demanding, and can frequently be seen at the very entrance to the nest-hole. In situations where the nest is adjacent to a flat surface, as it is here, they will even come right outside the hole to be fed by the parents. By now, the white gape-flanges, so conspicuous in the first week or two of life, have all but disappeared, and the young Hoopoe looks very like its parents, although its bill is still somewhat shorter and less decurved. The young are now being fed by both parents, and receive up to 50 feeds daily. Because the eggs hatch asynchronously, however, the chicks vary in size; as a result, the younger ones, being smaller, receive less food than their older nestmates and develop more slowly than do older chicks, and it is by no means uncommon for one or more to die through starvation. Once they have left the nest for good, fledglings will continue to be fed by their parents for several days, and accompany them for a few weeks or more, but they are able to forage independently within a week. This is important, as the parents often start a second brood and then have to leave the young of the first to fend for themselves. Many Hoopoes do not breed until they are two years old, but a variable number mate and rear their first young when they are one year of age. Breeding success is relatively high, with fledged broods in Europe containing four young on average, and sometimes five or more young being successfully reared.

[*Upupa epops epops*,  
Provence, France.  
Photos: Guy Bortolato/  
Bios]



This well-developed nestling, eagerly anticipating a feed, is almost ready to leave the nest. Apart from its somewhat shorter bill, and vestiges of the gape-flanges around the bill base, it is effectively identical to the adult, although the less worn condition of its feathering is apparent. The way in which the nestling almost fills the entrance hole recalls an interesting development in the behaviour of the adult female. Once the eggs have hatched, she often prevents her mate from entering the nest by standing at the entrance hole with crest raised and body feathers ruffled. The deep rufous plumage coloration of the southern African race is evident in this photograph, and also noticeable is the absence of white subterminal spots on the crest feathers.

[*Upupa epops africana*,  
Helderberg Nature Reserve,  
Somerset West,  
South Africa.  
Photo: Peter Steyn/Ardea]



truder in the nest, usually aiming steeply upwards, and with the jet of foul liquid covering a distance of 25-60 cm. Both the cloacal ejection and the olfactory defence can occur simultaneously. Moreover, the young birds, holding the crest raised, leaning forward on the breast, and with tail cocked and expanded, emit snake-like hisses, and they make sudden sharp jabs with the bill. Such is the stench that arises from the nest that the phrase "stink like a Hoopoe" is a term of abuse in some rural areas of central Europe. There is, however, a mistaken view that it is the parents' neglect of sanitation that causes all Hoopoe nests to smell powerfully. In fact, the female regularly removes the chicks' droppings, tossing them through the nest entrance, and the chicks themselves later often defecate through the nest entrance. It has been suggested that it is only if the anti-predator responses have been triggered that the nest acquires its malodour.

On the other hand, and despite the female's often considerable early efforts at nest sanitation, the nestlings will habitually defecate along the rear wall of the cavity, so that the nest-hole can quickly become foul-smelling. Sometimes, a residue of dry faeces 10-25 cm deep has built up in the hole by the time the young fledge. The smell may intensify if, as sometimes happens, a dead chick is not removed from the nest. It is relevant to note that, frequently, the first action of newly fledged Hoopoes is to take a sand-bath. The fledglings beg for food for a brief period only, coming to the ground to probe for food after about six days.

Normally, Hoopoes rear just one brood in a season, but there can be two or even, rarely, three broods. Replacement clutches are routinely laid after nest predation or loss at the egg stage, but in south-east Spain, for example, only 19% of females laid a second clutch after raising one successful brood, as compared with up to 57% in Germany. A second clutch starts within days of the first brood fledging. In such cases, the male may feed the fledglings alone for the last few days. The incubating female shows considerable hostility towards young of the first brood if they come too near the nest. Depending on whether one or two broods are raised, juveniles remain together with their parents in a loose family party for some weeks and, in Egypt, even some months after fledging.

Breeding success seems to be relatively high. Of some 172 eggs laid in 24 nests in central Europe, 74% hatched and 58% produced fledglings; an average of 5.2 young hatched from a mean clutch of 6.9 eggs, and an average of 4.3 young fledged per nest. There is some evidence that both the frequency of second broods and the total breeding success are related, at least in part, to the number of elements in the male's song phrases (see Voice).

The Hoopoe appears to breed for the first time at one year of age, although some, or perhaps many, individuals probably do not do so until they are two years old.

## Movements

The Hoopoe's pattern of movements is somewhat complex across its wide area of distribution. Not surprisingly, it is a migrant in the northern part of its range, from Europe eastwards across large areas of Siberia, but even in less seasonal regions it is as often a partial migrant as it is a resident. Resident populations, always allowing for short-distance dispersal in response to local conditions, include the North African and Canarian representatives of the nominate race, and the subspecies *major* from Egypt and northern Sudan, *marginata* in Madagascar, and *longirostris* in easternmost south Asia and South-east Asia. Most members of the subspecies *ceylonensis* of the Indian Subcontinent and Sri Lanka are also residents, although the western populations of that race tend to move between the Himalayas in the summer and the deserts of Sind and Rajasthan in the winter. Populations of nominate *epops* breeding in the Middle East and east to Pakistan appear to be resident, but it is possible that this is an illusion created by their replacement in winter by immigrants from farther north.

African populations, like Indian ones, show somewhat complicated responses depending on local, regional and larger-scale temporal conditions. In the Sahelian zone the subspecies *senegalensis* is resident, but it is partially migratory farther north



Hoopoes are frequently encountered in man-altered habitats, especially around farms or where dilapidated walls and old buildings are present. Indeed, in many parts of their range they are more numerous in such areas as traditionally managed farmland, vineyards, orchards, olive groves and cultivated plains than they are in other, more natural landscapes. Man-made structures, whether inhabited or not, provide a ready supply of nesting sites, which are eagerly exploited by a number of bird species. Hoopoes, for example, not uncommonly nest in recesses in farm buildings, which offer a relatively warm and safe breeding environment, as well as a reliable nearby supply of food in the form of invertebrates and small reptiles. Because this attractive species consumes many insects regarded by humans as crop-damaging pests, including cockchafer, certain orthopterans and a variety of caterpillars, it is generally a popular bird and is protected by law in many countries. Since the middle of the twentieth century, however, the modernization and intensification of farming, with the removal of trees and hedges and the large-scale use of pesticides, have led to reductions in the availability of nest-sites and insects, resulting in a decline in the populations of this and many other avian species.

[*Upupa epops epops*, Fülöphaza, Kecskemet, Hungary.  
Photo: Peter Bracht]

and south; the most northerly records are from the wet period in August, and the most southerly ones are from the dry season in February, in south Nigeria and north Cameroon. The subspecies *waibeli* of the forest-savanna mosaic north of the Congo Basin visits East Africa during November to March, but it is by no means clear what proportion of the total population undertakes this displacement. Also in East Africa, the race *africana* is resident in the highlands; is present in Tsavo in December-June, and farther south, in Tanzania, in July-December; and is common in north-west Tanzania in April-August. South African Hoopoes, also of the subspecies *africana*, may be partial migrants, some moving to Zimbabwe and southern Mozambique for the non-breeding season. The species is a year-round resident in various parts of South Africa, but it can be twice as common in the spring months of September to November as it is in the austral autumn of March-May.

Although small numbers of European Hoopoes spend the winter in North Africa and the Mediterranean Basin, with a few occasionally remaining in southern France, ringing recoveries show that the majority of that population winters in sub-

Saharan Africa, south to Uganda and northern Kenya, where they intermingle with the local *senegalensis*. Migration appears to be both diurnal and nocturnal, and takes place on a broad front through the Mediterranean region and probably also over the Sahara, although the birds certainly use the Nile Valley and major oases. Hoopoes breeding in the western half of Europe appear to travel through the south-western landmasses of Iberia and Italy, while those in the eastern half move through the Balkans.

Migrant West Palearctic Hoopoes are notoriously vague in their schedules, and individuals commonly linger late into the year and reappear early in the following spring. This is presumably related to the relatively short distances that some birds travel, and to the relatively broad niche that the species can exploit, both digging for larvae and snapping up ground-haunting Orthoptera (see Food and Feeding). The autumn migration is particularly protracted, beginning as early as mid-July and lasting until late October, although there is a distinct peak in movement in September. The spring migration starts from the winter quarters in mid-January, with birds crossing major barriers, such



as desert and mountain areas, on a broad front in mid-March. Migrants typically occur singly or in small, loose parties, but more than 100 have been recorded in a strung-out group in the Nile Valley.

At certain seasons and places in Africa or southern Asia, two or more subspecies occur together. These are nominate *epops* and *senegalensis* in Sahelian regions, *waibeli*, *africana* and probably *senegalensis* in eastern Africa, nominate *epops* and *ceylonensis* in the Indian subcontinent, and *longirostris* and *saturata* in South-east Asia. Nevertheless, breeding sympatry has never been documented. Relationships among the subspecies in these areas are poorly understood. The southern limits of northern migrants visiting the tropics, and the northern limits of southern migrants, are documented only schematically.

When anticyclonic conditions dominate during the northward return passage, Hoopoes of the nominate race fairly regularly overfly their breeding areas and appear, albeit usually only briefly, in northern Europe. On occasion, however, such individuals remain long enough to breed in these northern parts, well north of their normal breeding range in Europe. In Asia, Palearctic populations winter as far south as the outer northern tropics; vagrants have reached the lower Malay Peninsula, north-east Sumatra, north-west Borneo and the northern Philippines. Finally, a Hoopoe of the nominate race, present on Picard, Aldabra, in October 1999, was only the second record of this species to have been officially documented for the Seychelles, the first having involved the Afrotropical race *africana*.

### Relationship with Man

The distinctive plumage, appearance, flight and voice of the Hoopoe have won it a special place in human affections, and a long tradition in human culture. It appears as a hieroglyph and was revered as sacred in ancient Egypt, it figures prominently in Aristophanes' play "The Birds", and it features widely in folklore.

In one Greek myth, the bigamous Thracian king Tereus, when pursuing his wives, the sisters Procne and Philomela, with an axe, is turned into a Hoopoe and they, respectively, into a swallow (*Hirundo*) and a nightingale (*Luscinia*). The "hoop hoop" calls are his cries of "where, where?" as he searches in vain for his lost brides. Under the name "dukupath", mistranslated in the English-language version of the Bible as "lapwing", the Hoopoe was pronounced unclean under Jewish law, but in some countries of southern Europe these birds, fattened at the start of the autumn migration, were regarded as a delicacy, particularly by the Christians of Constantinople. In Arabia, the species was revered for its medicinal qualities, its head being used in charms. In modern times, its striking appearance, familiar to many people throughout the Old World, has resulted in its being used as the brand or logo of various businesses and ornithological societies.

The Hoopoe's diet includes a number of insects considered detrimental to man. In north-east Spain, for example, C. Stefanescu recorded Hoopoes feeding on the pupae of Pine Processionary Moths, one of the most important forestry pests in southern Europe. The moth's caterpillars feed on the needles of a wide variety of pines (*Pinus*) and other conifers, both natural and introduced, and during "plagues" can cause losses of up to 35% of the annual growth. Interestingly, the pupae, having been extracted from the ground by the Hoopoes, were also seized and eaten by Woodchat Shrikes (*Lanius senator*), which clearly benefited from the former's activities.

The Hoopoe's usefulness as a controller of various agricultural and forestry pests, such as cockchafer, certain crickets and grasshoppers, and various phytophagous caterpillars, has been recognized in many areas. The Hoopoe is consequently very widely protected by national law. Even so, there are certain countries in which passage migrants are still quite heavily persecuted by hunters. Elsewhere, by contrast, people enhance the breeding prospects of the species in given areas by providing nestboxes. Its use of nestboxes has been documented across a wide range from northern Europe to Japan, where population

densities are not so high as they are in its Mediterranean strongholds.

The species adapts relatively well to captivity, and has been bred repeatedly by several avicultural institutions and many private individuals. It is also, however, an object of the illegal bird trade, and in some parts of its European breeding range more Hoopoes can be found in captivity than can be observed in the wild. This was the case, for example, in 1991 in south-west Germany.

### Status and Conservation

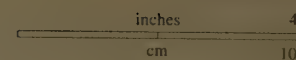
In general, the Hoopoe remains a fairly common to locally common bird throughout its range. At least at the fringes of this range, however, it has suffered some very obvious losses. In the middle of the nineteenth century it was, for example, distributed widely and commonly across central Europe, breeding in southern Denmark and Sweden, but in the following hundred years it showed a marked withdrawal southwards, dying out as a breeding bird in these countries and in Belgium, the Netherlands and much of Germany.

Since the 1950's the species appears to have maintained its range, but it has continued to diminish, if perhaps relatively slightly, in numerical strength. Decreasing trends have been reported throughout Europe, especially in peripheral populations, but also in some strongholds such as France, Ukraine, Romania and Greece. This long-term trend is strikingly similar to that of the Lesser Grey Shrike (*Lanius minor*) and that of the European Roller (*Coracias garrulus*), species which partly share the same habitats and food types as the Hoopoe. In 1994, the Hoopoe was judged to be secure in Europe, with a minimum population of 670,000 pairs, although more recently some 700,000-900,000 breeding pairs have been estimated for the continent, with between five million and ten million birds worldwide.

Changes in farming practices since the 1950's probably account for the downward population trends in various areas of Europe. In particular, the removal of trees and hedges has led to the loss of nest-sites, while large-scale applications of insecticides reduce the abundance of such prey as the larger crickets, grasshoppers, cockchafers, scarabaeid beetles and caterpillars. The marked reduction in the extent of low-intensity, small-scale farming must also have had a great impact in the cultivated parts of the species' breeding range. Desertification and some changes in vegetation cover and climate brought about by high-intensity farming may also have contributed to a decline in Asia, Africa and Madagascar. In the Thai-Malay Peninsula, the race *longirostris* was once locally common, including on the island of Phuket, but it is now sparse, local and apparently in retreat northwards, with no modern breeding records. In that region, however, it is hunting and disturbance by humans that appear to be responsible for this situation.

The reversal of the Hoopoe's slow but widespread European decline can be achieved only through wide-ranging changes in agricultural practices, involving the promotion of non-intensive farming and the return of intensively used farmland to pastures and meadows with scattered trees. A decrease in the use of insecticides would probably also be a very effective conservation measure. In particular, the planting in open pastures and meadows of trees which eventually produce nesting cavities, such as are found in pollard willows (*Salix*), or the deployment of special nestboxes in areas where there is a lack of natural cavities, may go some way towards supporting the species. Hoopoes also need help in Africa and Asia, where increasing agricultural utilization of savanna and steppe regions may have already begun to, or is poised to, cause a decline in its numbers, particularly through overgrazing, which destroys or degrades the cover of trees and bushes. At the very least, studies of Hoopoe abundance under various natural and farming regimes are required, in order to ensure that management options for the species are understood and used wherever possible.

Meanwhile, it is also high time that the persecution of migrant Hoopoes in southern Europe and parts of Asia was brought properly under control.



## PLATE 32

## Family UPUPIDAE (HOOPOE) SPECIES ACCOUNTS

### Genus *UPUPA* Linnaeus, 1758

#### Hoopoe

##### *Upupa epops*

French: Huppe fasciée

German: Wiedehopf

Spanish: Abubilla

Other common names: Common/Eurasian Hoopoe; African Hoopoe (*africana*); Madagascar Hoopoe (*marginata*); Ceylon/Indian Hoopoe (*ceylonensis*)

**Taxonomy.** *Upupa Epops* Linnaeus, 1758, Sweden.

Madagascan form *marginata* widely treated as a separate species on basis mainly of distinctive territorial call. Race *africana* also considered a full species by some, based on varying amounts of white in wing, and other minor differences of colour pattern (possibly also between sexes), but linked to race *senegalensis* by intermediate race *waibeli*. Races *saturata* and *ceylonensis* intergrade with nominate. NW Indian Subcontinent population sometimes separated as race *orientalis*, but now generally regarded as inseparable from nominate; paler birds in S & E South Africa sometimes separated as race *minor*, but validity requires confirmation. Nine subspecies currently recognized.

##### **Subspecies and Distribution.**

*U. e. epops* Linnaeus, 1758 - NW Africa, Canary Is and Europe E to SC Russia (Ob-Yenisey watershed), NW China (Sinkiang) and NW India.

*U. e. major* C. L. Brehm, 1855 - Egypt, N Sudan and E Chad (Ennedi).

*U. e. senegalensis* Swainson, 1837 - S Algeria (Ahaggar), and dry belt from Senegal E to Ethiopia and Somalia.

*U. e. waibeli* Reichenow, 1913 - Cameroon and N Zaire E to Uganda and N Kenya.

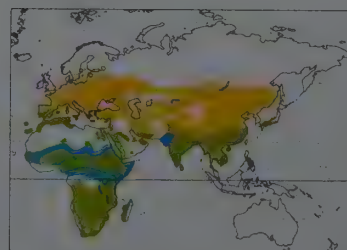
*U. e. africana* Bechstein, 1811 - C Zaire E to C Kenya, and S to the Cape.

*U. e. marginata* Cabanis & Heine, 1860 - N, W & S Madagascar.

*U. e. saturata* Lönnerberg, 1909 - SC Russia (E of R Yenisey) E to Japan, and S to C China and Tibet.

*U. e. ceylonensis* Reichenbach, 1853 - plains of Pakistan and N India S to Sri Lanka.

*U. e. longirostris* Jerdon, 1862 - Assam and Bangladesh E to S China, and S to N Malay Peninsula and Indochina.



**Descriptive notes.** 26-32 cm; 47-89 g. Unmistakable, with long, thin, decurved bill (5-6 cm), large crest, black-and-white rounded wings, and broad black tail with white band near base; in flight, white (or creamy white) and black bands on inner wing, wholly black primary coverts, black primaries. Male nominate race pale sandy-buff, tinged pinkish below, feathers of crest with white subterminal spots and black tips; white band across tips of primaries, white tips on inner primaries; bill grey, legs rather short, flesh-grey to dark grey. Sexes similar except female slightly smaller and duller, throat more whitish. Ju-

venile like female, but crest and bill shorter and duller. Races vary mainly in size, depth of



coloration and some other details, most of S ones lacking white subterminal spots on crest feathers: *saturata* similar to nominate, slightly greyer on mantle, slightly less pink-tinged below; *ceylonensis* smaller, more rufous, crest without subterminal white; *longirostris* larger, somewhat paler than last, white wingbars narrower; *major* larger, bill longer, upperparts greyer, tailband narrower; *senegalensis* small, wings shorter, more white on secondaries; *waibeli* like previous but darker, slightly more white in wing; *africana* very deep rufous, secondary bases fully white on male, almost so on female (unless sex difference age-related), no white bar across outer primaries; *marginata* larger and much paler than previous, white secondary bars very narrow, white tailbar narrower, white bar across primaries.

**Habitat.** Open country such as pastures, parkland, orchards, sand-heathland, olive groves, vineyards, also steppe and broken ground in Asia, and dry and wooded savanna in Africa and Madagascar; favours short-grass sward or bare ground, with scattered trees or cliffs to provide holes for roosting and nesting. Requires presence of features offering perches, shade, nest-sites and accessible food; frequently found around villages and in traditionally farmed areas. In Madagascar, open or disturbed lowland areas up to 1500 m, either in open areas along coastal plain and adjacent to littoral forest, or in spiny forest and even gallery forest; commonest in well-wooded forest margins; in dry areas, appears to prefer slightly degraded and more open forest.

**Food and Feeding.** Mostly larger insects and their soft soil-dwelling larvae and pupae; body size of prey rarely exceeds bill length. Crickets (Gryllidae), mole-crickets (Gryllotalpidae), other Orthoptera, beetles (mainly coprophagous scarabaeids and zoophagous carabids), phytophagous caterpillars, also spiders, termites, ants, locusts, ant-lions (Myrmeleonidae), *Tipula* larvae, shieldbugs, centipedes; also spiders. Also small vertebrates up to 15 cm long, e.g. lizards, snakes, frogs, geckos. Usually forages alone, or pairs feed in close proximity. Forages mostly on ground, digging and probing with bill in soft earth; also turns over leaves and other debris, probes in refuse and dry dung for insects and invertebrates, and occasionally pokes at carrion. Occasionally uses bill to prise off tree bark, or forages among lichen on branches.

**Breeding.** Season Jan/Feb-May in Palearctic, mostly Aug-Jan in E Africa, Sept-Dec in Madagascar, and Jan-Jun in Malay Peninsula; in S areas double-brooded, possibly triple-brooded, Monogamous, solitary and territorial breeder; home range 20-70 ha. Nest in natural hole in stump, tree, wall, old building, or cliff, or among boulders, unlined or slightly lined; sometimes in nestbox. Eggs 4-7 in tropics, 5-8 in Palearctic, laid daily; incubation by female, period 16-18 days; nestling downy in first 3-5 days, later covered in long spiny quills, crest developing by day 14; at 20-24 days chicks sit in nest entrance; nestling period 26-32 days in South Africa, 24-28 days in C Europe and Asia. Breeding success relatively high: in C Europe, 172 eggs laid in 24 nests produced average of 4.3 fledglings per nest; using nest-boxes, first broods in E Germany averaged 4.4-5.3 young fledged per nest, those in SW Switzerland 4.8-5.7, whereas second broods in E Germany averaged 3.2-3.6; rarely, 7 chicks raised from single brood. First breeding at 1 year, perhaps at 2.

**Movements.** N populations migratory, most others partially migratory; nominate *epops* in NW Africa and Canary Is and race *major* in Egypt and N Sudan more sedentary; *marginata* resident in Madagascar. Nominate *epops* from W Palearctic winters in sub-Saharan Africa S to about Kenya, with few farther S, while E Palearctic populations generally move shorter distances S to S India and China; autumn passage peaks in September; can cross higher altitudes, recorded at up to 6400 m in Himalayas; return starts mid-Jan to Mar; in N Mongolia, earliest arrival on breeding grounds in mid-Apr, when still winter conditions there. Rare straggler S to N Sumatra, NW Borneo and N Philippines.

**Status and Conservation.** Not globally threatened. Over 700,000 breeding pairs thought to occur in Europe alone (strongholds in Iberia, with up to 600,000, and France, with c.30,000), and a further c. 158,000 in European Russia; total world population recently estimated at 5,000,000-10,000,000 birds. Distinctive Madagascan race *marginata* common in N (S limit Antalaha), W & S of that island, rarer on High Plateau (Antananarivo, Ambalavo), and locally common in SE. Protected in most countries; in some listed as highly endangered (e.g. Germany), in more countries regarded as vulnerable or endangered. Decreasing trends reported in Europe, especially in peripheral populations, but also in such strongholds as France, Ukraine, Romania and Greece. Range contraction towards S combined with decline in numbers in most European countries evidently part of longer-term trend apparent since late 19th and early 20th centuries. In past, locally common in N Malay Peninsula, where appears to have declined notably, probably as a result of hunting and disturbance; no recent evidence of nesting, and most recent records may refer to migrants. In Germany, species is good bio-indicator for areas of sand-heathland (typically abandoned military areas), where sometimes present at high densities. Hunted in Mediterranean region and in parts of SE Asia.

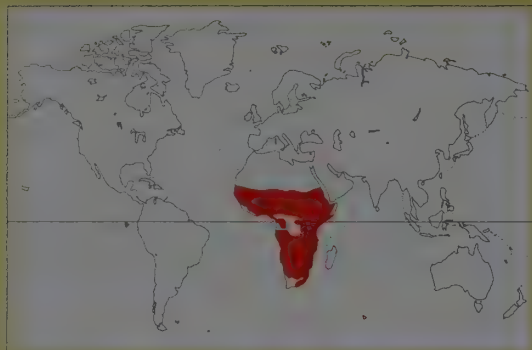
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## Class AVES

## Order CORACIIFORMES

## Suborder BUCEROTES

## Family PHOENICULIDAE (WOODHOOPES)



- Medium-sized arboreal birds, generally black, often iridescent, with or without white in wings and tail; bill forceps-like, usually decurved, specialized for obtaining arthropod prey in fissures and cracks in tree bark.
- 21-38 cm.



- Sub-Saharan Africa.
- Wooded habitats, from tropical lowland rainforest to arid bush country.
- 2 genera, 8 species, 24 taxa.
- No species threatened; none extinct since 1600.

## Systematics

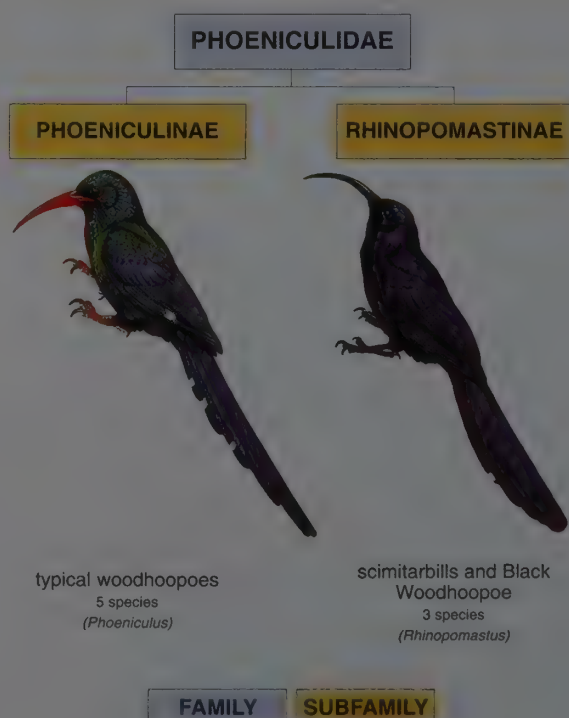
The woodhoopoes, which comprise the family Phoeniculidae, form an ancient and distinctive group of medium-sized to smallish non-passerine birds. Although the family currently occurs only in sub-Saharan Africa, a phoeniculid-like bird has been identified from the Eocene of England, and phoeniculids have been reported from the early Miocene of Bavaria and France. It appears, therefore, that the present-day distribution of the family is a relict of the past range, as is also the case for some other groups that are nowadays likewise found only in tropical and subtropical Africa. For example, the mousebirds (Coliidae) and the turacos (Musophagidae), which today are restricted to sub-Saharan Africa, are both known from the Miocene of France.

Currently, the taxonomy of these birds is in a state of flux. Woodhoopoes present some interesting and unresolved problems at all levels of classification, from ordinal and familial to generic, specific and subspecific. Taxonomic treatments of the Phoeniculidae have typically employed from one to three genera. C. M. N. White and D. W. Snow placed all species into a single genus, *Phoeniculus*, as did J. D. Ligon and N. C. Davidson in a more recent treatment in 1988. At the other extreme, older works often employed three genera, *Phoeniculus*, *Scoptelus* and *Rhinopomastus*. In the light of DNA-DNA hybridization studies carried out by C. G. Sibley and J. E. Ahlquist, the best solution may be the recognition of two genera, each comprising a subfamily. In this treatment, the subfamily Phoeniculinae, comprising the genus *Phoeniculus*, includes five species of "typical" woodhoopoes, while the subfamily Rhinopomastinae is represented by the genus *Rhinopomastus*, containing two species of scimitarbill plus the Black Woodhoopoe (*Rhinopomastus aterrimus*). It is perhaps worth stressing that the long-established vernacular name of woodhoopoe given to this last-mentioned species does not reflect what is now considered to be its phylogenetic relationship within the family; however, it seems inappropriate to rename the species Black Scimitarbill, as some have proposed, given that its bill-shape is far from living up to this epithet.

Traditionally, the family Phoeniculidae has been placed within the order Coraciiformes. Within this group, the woodhoopoes are most closely related to the hoopoes (Upupidae). In 1975, A. Feduccia discovered that these two groups share a unique, derived stapes morphology. They also share a long, rather thin, decurved bill. Certain aspects of the breeding biology of the two

groups likewise are similar: both are hole-nesting, and the nest is often foul-smelling as a result of runny excrement combined with an odoriferous substance secreted from the oil-gland by startled chicks. Ecologically, as well as in external appearance, the two groups are very different. All phoeniculids are arboreal foragers, whereas hoopoes feed almost exclusively on the ground. Associated with this difference in foraging behaviour, the woodhoopoes hop rather than walk when they are on the ground, while hoopoes walk strongly.

Most modern taxonomic treatments ally the woodhoopoes and the hoopoes with the hornbills (Bucerotidae), and in many traditional treatments these three groups comprise the suborder Bucerotes within the order Coraciiformes. However, the DNA-DNA hybridization studies by Sibley and Ahlquist, and anatomi-



Subdivision of the  
Phoeniculidae

(Figure: Hilary Burn)



cal studies by P. J. K. Burton, have led to the recommendation that the woodhoopes and the hoopoes be placed in their own order, the Upupiformes. This major higher-level taxonomic revision has recently been adopted by the American Ornithologists' Union.

More surprisingly, Sibley and Ahlquist's studies suggest that the typical woodhoopes (*Phoeniculus*) should be separated at the family level from the scimitarbills and the Black Woodhoopoe. Following this proposal, the two families would be the Phoeniculidae and the Rhinopomastidae. Separating these birds into two families is an interesting conclusion in view of their obvious similarities in appearance, which hitherto have been taken as indicative of close phylogenetic relationships. If correct, the DNA studies suggest that, over evolutionary time, genetic differentiation of these two lineages has proceeded farther than has morphological differentiation: in other words, morphological divergence has been very conservative. Notwithstanding the external similarities between the two genera, it seems sensible meanwhile to separate them tentatively into two subfamilies, Phoeniculinae and Rhinopomastinae, in order to emphasize that, genetically, they differ considerably. Perhaps the morphological resemblances between these two groups simply reflect the fact that all of the living species are quite similar in their unusual ecology and mode of life. All woodhoopes and scimitarbills are arboreal, and in their behaviour and anatomy all exhibit special adaptations for foraging primarily on the surfaces of trunks and branches of trees, using the specialized bill to probe for arthropods in crevices and beneath bark (see Morphological Aspects, Food and Feeding).

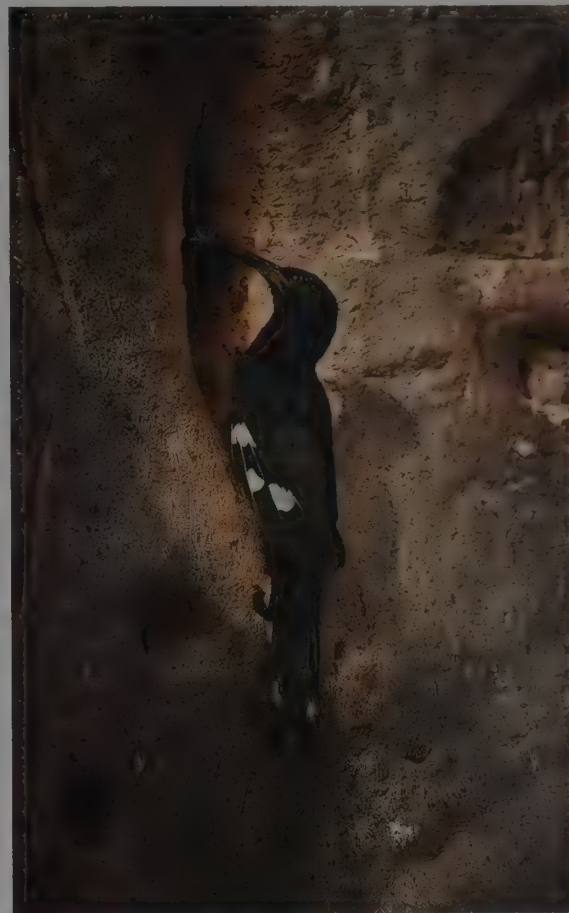
The DNA evidence suggests that *Phoeniculus* and *Rhinopomastus* separated 10.2 million years ago, during the Miocene. With only two genera, it is difficult to ascertain which is the more primitive and which is the more derived. Their morphological specializations appear to be similar, apart from the more extreme development of the bill in the scimitarbills. The Rhinopomastinae are characterized in part by their relatively quiet vocalizations and unobtrusive behaviour, which contrast conspicuously with the noisy, group-living habits of the Phoeniculinae, although the enigmatic Forest Woodhoopoe (*Phoeniculus castaneiceps*) is an exception in this respect. The social behaviour of the typical woodhoopes differs from that of the scimitarbill group in that most or all species exhibit a highly complex level of sociality, or group-living, which in at least some, and possibly all, species is associated with co-operative breeding. Within the genus *Phoeniculus*, co-operative breeding may be a "primitive" trait, in that at least four of the five species appear to exhibit such behaviour. This suggests that co-operative breeding was present early in the history of *Phoeniculus*, but after the split from the lineage leading to today's *Rhinopomastus* species.

The most puzzling species taxonomically is the Forest Woodhoopoe. Although it does not clearly fall into one genus or the other, it is probably best treated tentatively as a species of *Phoeniculus*, even though it shares certain characteristics with members of both genera. This fact led Snow to suggest that the Forest Woodhoopoe may be the most primitive living member of the group. Some individuals of this species possess a white head, indicating a possible affinity with the White-headed Woodhoopoe (*Phoeniculus bollei*). This feature, together with the greenish gloss to the dark plumage, suggests that the Forest Woodhoopoe belongs with the other members of *Phoeniculus*. On the other hand, its small size, bill shape, bill and leg colours and voice more closely resemble those of the genus *Rhinopomastus*. These traits prompted Davidson to ally the Forest Woodhoopoe with the species of *Rhinopomastus*. In view of the DNA-based conclusion that the woodhoopes and the scimitarbill group are so distinctive that they should be separated at the family level, as outlined above, future studies of the molecular genetics of all species may readily determine whether the Forest Woodhoopoe is more closely related to *Phoeniculus* or to *Rhinopomastus*.

At the species level, both the woodhoopes and the scimitarbills pose some interesting systematic problems. One of the major ones involves the Green Woodhoopoe (*Phoeniculus*

Two or more races are accepted for each of the eight phoeniculid species, reaching a peak in the Green Woodhoopoe, with six currently accepted races that differ in body size, plumage coloration, and the amount of white in the wings and tail. Adults of five of these races have a bright red bill, but those of the race *senegalensis* typically have a black bill, as here. Some authors consider the Green Woodhoopoe to constitute a superspecies with the Black-billed (*Phoeniculus somaliensis*) and Violet Woodhoopes (*P. damarensis*), but these taxa may instead reflect complex variation within a single species.

[*Phoeniculus purpureus senegalensis*, near Marondera, western Gambia. Photo: William Paton/ NHPA]



*purpureus*). This species' range comes into contact with those of two other, very similar populations that are usually accorded specific rank, namely the Black-billed Woodhoopoe (*Phoeniculus somaliensis*) and the Violet Woodhoopoe (*Phoeniculus damarensis*). These three forms, often considered to constitute a superspecies, differ in the colour of their iridescent plumage and in the colours of the tarsus and bill. Sibley and B. L. Monroe, however, expressed the view that the three are probably conspecific.

The decision to rank the Green, Black-billed and Violet Woodhoopes as full species appears to be based on the fact that birds identified as, respectively, Green and Black-billed Woodhoopes have been collected in the same area on the same day, as also have Green and Violet Woodhoopes. These specimens have been viewed as evidence of sympatry between two species. In the case of these birds, however, such interpretations may or may not be correct. Two points suggest that they are not. First, the extremely widespread Green Woodhoopoe exhibits considerable geographical variation in colour of the iridescent plumage and in bill length and colour, and all subspecies, some of which are distinctive, intergrade. Some of these subspecies differ from each other in much the same ways as Black-billed and Violet Woodhoopes differ from the Green Woodhoopes with which they come into contact. Secondly, the Green Woodhoopoe also shows considerable intra-population variation in these same traits: for example, related individuals from the same flock may differ in the green as opposed to purple sheen, as well as in bill colour. In short, questions concerning the specific status of the Green, Black-billed and Violet Woodhoopes are unresolved. Are the last two forms truly specifically distinct from the first, as well as from each other, or are they geographical variants of the Green Woodhoopoe? The highly unlikely geographical distribution of the Violet Woodhoopoe can be viewed as evidence for the latter interpretation. Its two populations, *damarensis* in the south-west and *granti* in the north-east, are separated by many hundreds of miles, and the assumption that they not only are conspecific but also are specifi-



cally distinct from the widespread and geographically variable Green Woodhoopoe strains credulity, perhaps especially in view of the several geographical races of the latter species. Even if the two forms *granti* and *damarensis* are more similar to each other in shades of feather colour than either is to typical Green Woodhoopoes, this does not really signal that they are more closely related to each other than they are to the Green Woodhoopoe, especially in view of the colour variation seen among the recognized subspecies of the latter. In particular, *damarensis* appears to be parapatric with the Green Woodhoopoe, making it reasonable to suggest that this population, at least, might best be considered a subspecies of the Green, as it was by A. Roberts.

As pointed out by Snow, careful field studies in the areas of putative sympatry will be required to determine the true situation. Simply documenting the presence in the same area of both green and violet-coloured individuals is insufficient to demonstrate that more than one species is involved. Until field studies of breeding birds, carefully quantifying both morphology and behaviour, have been conducted in areas of geographical overlap, the taxonomic status of these forms will remain subject to conjecture.

Another interesting case concerns the Common Scimitarbill (*Rhinopomastus cyanomelas*) and the Black Woodhoopoe. These two species have large and for the most part non-overlapping ranges, but in some areas of contact, as in southern Angola and south-eastern Zaire, they apparently intergrade. In western Zambia there is an almost continuous range of bill shapes, from the long, greatly decurved bill of *R. cyanomelas* to the shorter, straighter bill of *R. aterrimus*. This led Snow, C. W. Benson and M. P. S. Irwin to conclude that the two forms are conspecific. Again in western Zambia, however, they have been collected almost "side by side", and at any rate in parts of this region it appears that they are ecologically separated, with *R. cyanomelas* occurring in *Acacia* woodland and *R. aterrimus* in *Brachystegia*. For these reasons, and because of conspicuous differences in morphology, particularly bill and tail lengths, and in vocalizations, Davidson considers the two taxa to be specifically distinct, and to form a superspecies. At present, this seems to be the better alternative, as it is now appreciated that the occurrence of hybridization does not necessarily reflect especially close genetic relationships. Thus, despite documentation of limited interbreeding, designation of these two forms as separate species appears to be more firmly based than would seem to be the case for the Green, Black-billed and Violet Woodhoopoes.

Two or more subspecies are recognized for every species in the family. For the most part, the subspecies are distinguished by slight quantitative differences in colour or iridescence of the dark plumage, or in variation in the amount of white barring or spots on the wings or tail. An exception to this generalization is the subspecies of the Forest Woodhoopoe, which differ conspicuously in appearance (see Morphological Aspects).

The fact that geographical variation is fairly well marked in several species of phoeniculid probably reflects restricted movement by individuals, and thus restricted gene flow. In the Green Woodhoopoe, for example, the only species that has been studied in detail through large numbers of colour-ringed birds, most individuals are strikingly sedentary (see Movements), breeding either within their natal territory or no more than one or two territories away. This conservative pattern of dispersal, which may also be characteristic of other members of the genus, can, by reducing the extent and rate of gene flow, promote the kind of geographical variation in morphology that is used to distinguish subspecies.

## Morphological Aspects

As with most of the other families within the order Coraciiformes, the Phoeniculidae are morphologically distinctive. Once seen, no member of this small group can be confused with any other type of bird. The long, slender body and the long bill and tail of the woodhoopoes, together with their unique movement up the trunks and branches of trees, render them unmistakable. The tail, elongated but otherwise structurally unspecialized, is used both as a prop as the bird moves up tree trunks and branches,

and as a balance as it forages acrobatically on small twigs or other unstable substrates.

The plumage of phoeniculids is essentially black, often with some white barring or spotting on the wings and tail. The amount of white on the wings varies according to species, some having none at all and others having large, conspicuous white patches. The body plumage of adults of some species is highly iridescent, and with a primarily green, purplish (violet) or blue cast. At fledging, juveniles lack the iridescence of adults. In addition, in Green Woodhoopoes, some young birds, usually males, exhibit a brown throat. Exceptionally, the throat is very pale, contrasting strongly with the black plumage.

In all but one species, the males and females are similar in plumage. In the Forest Woodhoopoe, however, males of one subspecies are polymorphic, having the head green, brownish or white; in contrast, females have the head brownish-white. Thus, within the Phoeniculidae, the plumage of the Forest Woodhoopoe is unique on two counts: first, males show three morphs in the coloration of the head; and, second, females differ conspicuously from two of the male colour morphs.

Perhaps the most distinctive morphological characteristic of the Phoeniculidae is the bill. This is variably decurved, and in most species is long. In all species, the bill serves as a specialized, rather forceps-like foraging tool which permits extraction of arthropod prey from sites which are difficult of access, such as crevices in bark. As the vernacular name of the Common Scimitarbill suggests, it is in that species that the length and curvature of the bill are most pronounced. In some species, such as the Green Woodhoopoe, sexual dimorphism in bill length is conspicuous, with the bills of males averaging up to 20% longer than those of females, and the males' bills being also more decurved. Similarly, male Green Woodhoopoes average approximately 18% heavier than females. In correlation with these morphological differences, the male Green Woodhoopoe frequently forages on the trunks of trees, while the female more often gleans from the twigs and branches. In general, sexual dimorphism is more pronounced in *Phoeniculus* than in *Rhinopomastus*.

Variation in bill colour, both between and within species, is especially interesting in this group. In four species, the White-headed, Green and Violet Woodhoopoes and the Abyssinian Scimitarbill (*Rhinopomastus minor*), the bill of adults typically is red, while in the other four, the Forest, Black-billed and Black Woodhoopoes and the Common Scimitarbill, the bill is completely, or almost completely, black. Bill colour does not therefore correlate with phylogenetic position. Nor is it correlated with social system. The three red-billed species are highly social, but so, too, is the Black-billed Woodhoopoe. Conversely, the Abyssinian Scimitarbill is red-billed, but, like the Common Scimitarbill and the Black Woodhoopoe, which have a black bill, it is not a group-living species. The social life and breeding habits of the dark-billed Forest Woodhoopoe are unknown.

In all of the red-billed forms, the bill of juveniles is black, changing to red as the bird matures. Bill colour is thus correlated with the age of the bird. For example, in the Green Woodhoopoe, a species in which maturation of large numbers of marked, known-age birds has been studied, bill colour changes gradually from black to red over one to two years. Occasionally, older birds of either sex that have attained breeding status exhibit a considerable amount of black on the bill, this seeming to occur more frequently with males than with females. In the red-billed species, the progressive change of bill colour from black to red can help to account for interspecific, as well as intraspecific, variation in bill colour. Consider, for example, the Black-billed Woodhoopoe: because all of its closest relatives are red-billed, and because the base of its bill is sometimes red, it appears likely that the black bill of this species has been derived from a red-billed ancestor. If this is so, the bill colour may have evolved through the process of neoteny or paedomorphism, in other words the persistence into adulthood of a trait that is characteristic of immaturity. The genetic basis of bill coloration in the Black-billed Woodhoopoe may therefore be closer to that of its red-billed relatives than is implied by the conspicuous differences in the bill colours of adults.



The three *Rhinopomastus* species tend to exhibit less sexual dimorphism in size and appearance than do the typical woodhoopoes. Two of the three show a strongly decurved bill, as seen on this Abyssinian Scimitarbill. All three are solitary breeders, whereas the typical woodhoopoes of the genus *Phoeniculus*, social throughout the year, are probably all co-operative breeders. DNA work suggests that the two groups diverged over 10 million years ago, and some treat these two groups as separate families, while at the opposite extreme others lump the two genera together and place all members of the family in *Phoeniculus*.

[*Rhinopomastus minor*,  
Kenya.  
Photo: Dave Richards]



The wings of woodhoopoes are large in relation to the mass of the bird. The flight of phoeniculids is sometimes characterized in field guides by terms such as “floppy” or “jerky”, but these do not convey a complete picture of the birds’ aerial abilities, which themselves are not often observed. Although woodhoopoes are usually seen flying leisurely from one tree to another, this does not adequately reflect their powers of flight. The Green Woodhoopoe can fly strongly and swiftly for extended periods of time, and the same probably applies to the other species. Such periods of flight typically occur primarily when competing individuals or flocks engage in swirling aerial conflict. Sometimes this occurs far above the canopy of wooded savanna, and it may continue for many minutes. Only at such times are the truly impressive flying capabilities of these birds displayed.

In the White-headed, Green, Black-billed and Violet Woodhoopoes, the tarsi and toes of the adults are red, although, as with the bill, they are black in juveniles. In contrast, the legs remain dark throughout life in the Forest Woodhoopoe, the Black Woodhoopoe and the two scimitarbills. In all phoeniculids the tarsi are short and thick, which may be associated with the ability of these birds to hang upside-down while foraging, and in some species they may be largely feathered. As with the hoopoes, the third and fourth toes are fused basally. Woodhoopoes hitch up the trunks and branches of trees, much as do woodpeckers (Picidae), and, in accordance with their woodpecker-like movements over branches and trunks, their claws are well developed and sharply decurved. When on the ground, they do not walk as hoopoes do; rather, they move about by hopping. This pattern of ground locomotion, walking by terrestrial species and hopping by their arboreal relatives, is seen also among corvids and some other passeriform families.

Like many other tropical birds, the Green Woodhoopoe shows a lot of individual variation in its moult. In equatorial Kenya, the timing of moult is not synchronous among individuals, and it appears that, within a given population, some birds can be found in moult throughout most of the year, from February to November. Moult of individuals is a slow process, extending over a number of months. Because these birds may breed at almost any time, if environmental conditions are favourable, breeding and moult often occur simultaneously.

There are ten primaries, seven secondaries and ten rectrices. Primary moult begins with P1. Secondary moult begins with S7 and S1; the last secondary to be replaced is S4. The sequence of the tail moult is apparently erratic.

## Habitat

Members of the family Phoeniculidae have two essential habitat requirements. First, all woodhoopoes are almost exclusively arboreal and are tree-foraging specialists, searching for arthropods under bark and in crevices on the trunks and branches of trees. Second, all species require tree cavities for nesting, and, so far as is known, all also require cavities as nocturnal roost-sites. The phoeniculids are essentially therefore restricted to areas containing trees sizeable enough to contain such hollows. Although several species occupy dry bush country, in all cases some trees large enough to hold cavities suitable for roosting and nesting, as found in riverine gallery forest, must be present.

With these two basic requirements in mind, the major habitat types occupied by the various species can be grouped into three categories: forest, savanna and bush. Two species, the Forest Woodhoopoe and the White-headed Woodhoopoe, characteristically occupy true forest. The other species avoid forest proper, and are found instead in open woodland and savanna habitats; they include the geographically widespread Green Woodhoopoe and Common Scimitarbill, which occur in a variety of habitats ranging from woodland savanna to dry bush country. In contrast, the Black-billed Woodhoopoe and the Abyssinian Scimitarbill have relatively small ranges and are restricted to dry areas of *Acacia* bush and thorn-scrub, where they utilize the larger trees that occur along watercourses for nesting and roosting, as well as for foraging.

The two forest species, the Forest and the White-headed Woodhoopoes, occur sympatrically in suitable habitat across much of forested equatorial western Africa. Other pairs of phoeniculid species that occur sympatrically include the Green and White-headed Woodhoopoes, which can both be found where forest and savanna come together, while in drier areas the Green Woodhoopoe co-occurs with the Common Scimitarbill and the Abyssinian Scimitarbill. Similarly, in dry regions of Ethiopia,

the Black-billed Woodhoopoe may overlap with both the Black Woodhoopoe and the Abyssinian Scimitarbill.

Overall, south of the Sahara, one or more species of phoeniculid occurs in every area and in almost every habitat that has trees. Thus, by the measures of geographical range and diversity of habitats occupied, this small group of birds is a highly successful one.

### General Habits

All woodhoopoes are distinctly arboreal birds, spending most of each day foraging, often quietly, in the trees encompassed within their territories. Nevertheless, despite being adapted for an arboreal life, they may on occasion descend to the ground and even forage there, moving by hopping (see Food and Feeding).

A further example of the behavioural flexibility of the Green Woodhoopoe concerns the placement of the nest. All phoeniculids typically lay their eggs in tree cavities, but nests of that species have been found on the ground, in the roofs of houses and in the wooden mounting of an air conditioner (see Breeding).

The social systems of most phoeniculids have not been studied. It appears, however, that, with the possible exception of the Forest Woodhoopoe, members of the genus *Phoeniculus* are both highly social and highly vocal throughout the year, and it is probable that all of these species exhibit the social system known as co-operative breeding. White-headed Woodhoopoes are known to be co-operative breeders, and this kind of social system is well studied in the Green Woodhoopoe in different parts of its extensive range, from Ghana to Kenya and south to South Africa. In Kenya, Green Woodhoopoes live in groups of two to 16 individuals, with a mean group size of about 5.6 birds, the upper and lower size extremes being rare. Individuals making up the social groups of this species are usually genetically related, but birds unrelated to either member of the single breeding pair also occur regularly. Both related and unrelated "helpers at the nest" pro-

vide food to nestlings and fledglings, and assist in protecting the young birds from predators (see Breeding).

In contrast, members of the genus *Rhinopomastus*, the Black Woodhoopoe and the two scimitarbills, appear to be far less social than the *Phoeniculus* species, occurring as lone individuals, as pairs, or as pairs plus their recently fledged young. Although no member of this genus has been studied in detail, the few observations at nests of these three species indicate that co-operative breeding does not occur in this genus.

As previously noted, the breeding habits of the Forest Woodhoopoe are entirely unknown. Since it has been recorded in small groups of five or six individuals, co-operative breeding is a possibility; alternatively, such groups could be composed of a breeding pair and its recently fledged offspring. Documenting co-operative breeding in this species would provide important behavioural evidence to support its placement in the genus *Phoeniculus* (see Systematics).

Social units of Green Woodhoopoes are highly territorial, occupying the same area throughout the year and defending it daily against incursions from neighbouring groups. This is clearly seen in areas where suitable habitat is sufficiently extensive to provide space for several contiguous social units. In other situations, such as narrow strips of riverine forest or strips of *Acacia* woodland bordering lakes, territories are linear and densities of birds are much lower. As a result, confrontations between flocks occupying neighbouring territories are less frequent than they are in situations where a territory may have neighbouring ones on all sides of it.

The best-known social display of the Green Woodhoopoe has been labelled the "Rally". In this striking group display, the members of a flock perch close together, each one vigorously rocking back and forth with wings partly extended, raising and depressing the tail, while at the same time giving prolonged, loud vocalizations (see Voice). Although rallies are most intense during territorial encounters between neighbouring flocks, they occur at other times, too, as when flock-members are re-united. The rally is an intra-flock activity that serves to promote flock



Violet Woodhoopoes are gregarious throughout the year, living in groups of 2-12 individuals. These groups function as highly territorial units during encounters with neighbouring groups of conspecifics and when mobbing predators. Most group members are thought to be relatives, and group defence of the territory is likely to be important in allowing exclusive use of scarce but critical components of the habitat, such as the tree cavities used for nesting and roosting. The Violet Woodhoopoe probably breeds co-operatively, like the well-studied Green Woodhoopoe (*Phoeniculus purpureus*), but little is known about its breeding behaviour.

[*Phoeniculus damarensis damarensis*, Waterberg Plateau National Park, Namibia. Photo: Pete Morris]



unity and cohesion. The Green Woodhoopoe's close relatives, the Black-billed and Violet Woodhoopoes, along with the White-headed Woodhoopoe, also exhibit this conspicuous and fascinating group behaviour; whether the Forest Woodhoopoe ever engages in rallies is unknown. As the *Rhinopomastus* species do not live in groups, they do not exhibit this behaviour, which involves a number of individuals.

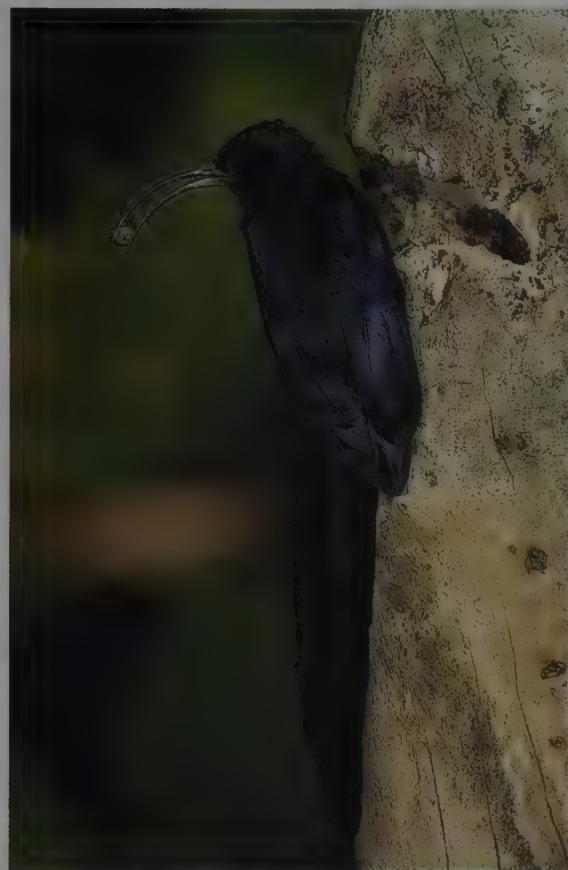
A related type of behaviour of Green Woodhoopoes is referred to as "Flag-waving". Flag-waving occurs during territorial encounters between flocks, just prior to a territorial confrontation. The "flag", in the form of a clump or lichens, a piece of bark, or a wad of spider web and frass, is picked up by one or two flock-members when intruders into the territory have been detected. The flag-waver, which is usually one of the breeders, waves the material to and fro, before flying towards the intruders ahead of the rest of its group. After alighting near the intruders, the flag-waver tends to position itself in front of its flock, thrusting the flag towards the trespassing group, which may be only a few feet away. Often, the defending group passes the flag back and forth among several individuals. Flag-waving appears to incite other flock-members and perhaps enhances co-ordination in aggressive defence.

Green Woodhoopoes may also carry flags in non-territorial contexts. When mobbing a potential predator, flock-members gather near it and give short, sharp alarm calls. Often, the birds cautiously approach the predator, with some individuals displaying more aggressively than others, arching the neck, drooping the wings, and fanning the tail while swaying backwards and forwards. The bolder woodhoopoes may carry flags, waving them as they sway before the predator. Here, too, the flag may be passed amongst several birds. As has also been suggested by A. Zahavi, it appears that risk-taking, both in territorial encounters and when displaying at predators, may be related to social status within the flock.

One of the most critical aspects of the biology of the Green Woodhoopoe is roosting behaviour, with several birds typically sharing a single cavity. Whether in equatorial Kenya or in more temperate South Africa, Green Woodhoopoes almost invariably roost in cavities; rarely, in an emergency, they will roost under bark. At Lake Naivasha in Kenya, which is at an altitude of about 1950 m, the nights are cool, and J. D. and S. H. Ligon proposed that these birds require cavities for roosting in order to ameliorate the low night-time temperatures. Green Woodhoopoes are "late risers" compared with many other species, and it appears likely that they remain in the cavity until air temperatures have started to increase. Certainly, basking in the early-morning sun is a commonly observed activity of this species.

Avoiding cool night-time temperatures is probably important to Green Woodhoopoes throughout their range. Energy savings associated with roosting in cavities have been quantified for this species in South Africa by M. A. du Plessis and J. B. Williams. When minimum nocturnal ambient temperatures are about 5°C, a woodhoopoe roosting with four others in a cavity can reduce its overnight energy expenditure by 30% or more. At a site in South Africa where nocturnal temperatures sometimes drop below freezing, such energy savings are thought to reduce mortality of adults during the winter months, when food is less readily available. Thus, an important benefit of cavity-roosting behaviour by the Green Woodhoopoe appears to be related to energy balance, and it seems that access to suitable cavities for roosting is critical to the wellbeing, and possibly even to the survival, of these birds. Consistent with this suggestion is the fact that Green Woodhoopoes are remarkably reluctant to leave their roost-sites. This makes it easy for the human investigator to capture them by climbing up to the cavity after dark, plugging the entrance, and the following morning placing over the entrance a clear plastic bag, into which the birds emerge. The roosting habits of other species of phoeniculid apparently have not been recorded, but they, too, probably roost in tree cavities.

In Kenya, obligate cavity-roosting by Green Woodhoopoes entails major costs, as well as thermoregulatory benefits. In the first place, while no cavity can deter the driver-ant, which is an important predator, relatively safe cavities, those likely to thwart



mammalian predators such as genets (*Genetta*), are a scarce resource, and one that affects the numbers and distribution of woodhoopoes on a local scale. Cavities are scarce in large part because they are also a requirement of numerous other species, including honeybees (*Apis*), other birds, and mammals. Secondly, roosting in cavities can apparently be dangerous as a result of the birds' vulnerability to arboreal nocturnal predators, of which genets are a prime example. Because of differences in body size, males and females often roost in different cavities; up to eight females have been recorded roosting together. Owing to their larger size, males have less choice of roost-sites and more often must roost in cavities of inferior quality, such as those in weak, rotten wood. Moreover, cavity entrances used by males must be considerably larger than those used exclusively by females, which in itself makes them less safe from mammalian predators, in particular. Mortality rates of male Green Woodhoopoes of all age and social categories, including breeders, helpers and immatures, are about 10% higher than those of females. This is probably due to differences in the security of the roost cavities used by each sex.

One of the most unusual characteristics of the Green Woodhoopoe, and one shared with the hoopoes, is the use of a malodorous oil from the uropygial gland as a predator deterrent. The smell of this oil is often detectable in museum specimens, including those of other phoeniculid species, which presumably, therefore, demonstrate similar behaviour. The oil-gland is unfeathered, except for a ring of small tuft-like feathers surrounding the opening at the tip of the papilla. At night, when a group of roosting birds is threatened, they may position themselves inside the cavity with their rear ends facing the entrance. The feathers of the lower back are then elevated, exposing the oil-gland, and a large drop of oil rapidly forms on the tip. This response to threats is also given by feathered nestlings. In addition, young woodhoopoes taken from the nest release copious amounts of foul-smelling, runny excrement.

The emission of uropygial oil in response to disturbance at the roost entrance strongly suggests that nocturnal predation by mammals is a selective force that has favoured the development

Most phoeniculids specialize on arthropods, using the tweezer-like bill to extract prey from fissures in the bark.

The birds generally move up the trunks of trees in much the same fashion as woodpeckers (Picidae), but the Common Scimitarbill is also known to move down the trunk, thus recalling the movements of nuthatches (Sittidae). This species is an acrobatic forager, sometimes hanging upside down as it searches for prey. All phoeniculids have an elongated tail to support them as they grasp tree trunks and to serve as a balance when they move about on small twigs and other unstable perches.

[*Rhinopomastus cyanomelas*, near Marondera, Zimbabwe.  
Photo: Peter Ginn/  
ARPS/APSSA]

of this unusual chemical defence mechanism. The frequency of predation at roost-sites indicates, however, that the woodhoopoes' chemical defence is not highly effective.

Green Woodhoopoes exist in a social environment composed of groups of co-operating individuals. This means that each individual bird is dependent on others in a variety of situations: (1) territories are defended by the group; (2) in Kenya, but not in South Africa, emigration of individuals from one territory to another is almost always accomplished by two or more birds of the same sex (see Movements); and (3) non-breeding helpers provide extensive assistance in the rearing of young, both before and after fledging. The outcome of most inter-group competitive interactions is dependent on relative sizes of the competing groups. Larger groups tend to dominate smaller ones, and very small groups composed of just two or three individuals often cannot successfully defend territorial space if neighbouring flocks are numerically superior. Alliances are therefore a critical component of an individual woodhoopoe's existence. This is clearly seen both in the group defence of the territory and, in Kenya, in the group emigration of two or more same-sex individuals to a breeding vacancy in a nearby territory. "Team" emigration greatly increases the chances that the team-members will be able to acquire and retain possession of the new territory in the face of competition and aggression from neighbouring groups. Although such emigrant teams are usually stable, an individual sometimes returns to the home territory. Once a group has moved into a new territory and established itself, the opportunity for additional individuals to join is almost non-existent, especially for males. On occasion, a team of two or three females will allow another one or two younger females to join it. Thus, in Kenya, woodhoopoes occupy a social environment where co-operative alliances are critically important. Typically, flockmates and emigrating unisexual groups of allies are relatives.

As a result of the high mortality suffered by these birds, however, an individual not infrequently loses its same-sex relatives. Because of the social environment of this population, with the prevalence of interdependence of individuals, lone birds are at an overwhelming competitive disadvantage. Under these circumstances, it appears that allying with an unrelated individual is a sound strategy, and one that is commonly employed. For example, out of 40 cases in which two or more birds of known genetic relationships joined forces to immigrate into a new territory, 22 teams were composed of kin individuals, while 18 were known to be composed of non-kin birds; of the latter 18, 14 were of females and four of males. In short, the formation of teams by unrelated birds, particularly females, is not a rare event and is clearly one kind of strategy for procurement of breeding space and social status.

Although mutual defence of the territory and team movement into a new territory are the most commonly seen forms of mutual aid, two other kinds of co-operation also occur. These involve individuals from one flock sometimes surreptitiously feeding fledglings in a neighbouring territory, and the feeding of adult flockmates by other flock-members. These aspects of behaviour have been interpreted as subtle strategies to promote the social status, in one way or another, of the donor of the food.

## Voice

The kinds, and probably the functions, of sounds rendered by the various phoeniculid species closely conform to their generic affiliation. Vocalizations are one of the most conspicuous and most important aspects of the behaviour of *Phoeniculus*. The social species in this genus, the White-headed, Green, Black-billed and Violet Woodhoopoes, characteristically are noisy birds, with vocalizations playing an important role in their social lives. In particular, group displays or "Rallies" (see General Habits) that function to promote cohesion within the flock rely in large part on synchronized vocalizations by each individual within the social unit. In contrast, the Forest Woodhoopoe and the three species of *Rhinopomastus*, namely the Black Woodhoopoe, the Common Scimitarbill and the Abyssinian Scimitarbill, are not highly social, and their calls are softer and far less noticeable to

the casual human observer than are those of the typical *Phoeniculus*. Even in some of these species, however, a number of calls have been recorded. The most common call of the Common Scimitarbill is a "poui-poui-poui", and three other calls have also been noted from that species: a high twittering "kui-kui-ker-ker", a harsh chattering "ka-ka-ka", and a low "ka" alarm call, the harsh chatter sometimes being accompanied by a bobbing up and down of the body, in a manner reminiscent of the woodhoopoes.

Several different kinds of call have also been recorded for the Green Woodhoopoe. An interesting aspect of this species' behaviour is that every vocalization given by an adult is sexually diagnostic, so that, to the experienced observer, a single-noted vocalization is sufficient to identify the sex of the bird. Male Green Woodhoopoes routinely emit "kuk" calls that are rather similar to the quack of a female Mallard (*Anas platyrhynchos*). These are usually uttered when the bird is alarmed, as by, for instance, a human observer who has approached too closely to the group; in similar circumstances, female flock-members give a higher-pitched "keek" call that is presumably homologous to the male's "kuk".

When a flock engages in a rally display, as at a territorial boundary, the birds give prolonged chuckling or cackling vocalizations, "kak-kak-kkkk". It is this vocal display that gave rise to the common name *kakelaar* and to the likening of the sound to the hysterical laughter of women (see Relationship with Man). During these displays, which involve all adult group-members, the calls given by each sex can be distinguished. It is possible, but not proven, that other woodhoopoes can ascertain the number of males and females in a rallying group. At the least, they should be able to determine by sound whether more than one male or female is present.

Males may also emit a call that sounds very much like a mammalian growl, and, interestingly, this vocalization is given in the kinds of contexts that elicit growls from other species. For example, the dominant male breeder may growl when it detects a neighbouring flock near or within its large territory. This individual then leads its group to a confrontation with the intruders.

## Food and Feeding

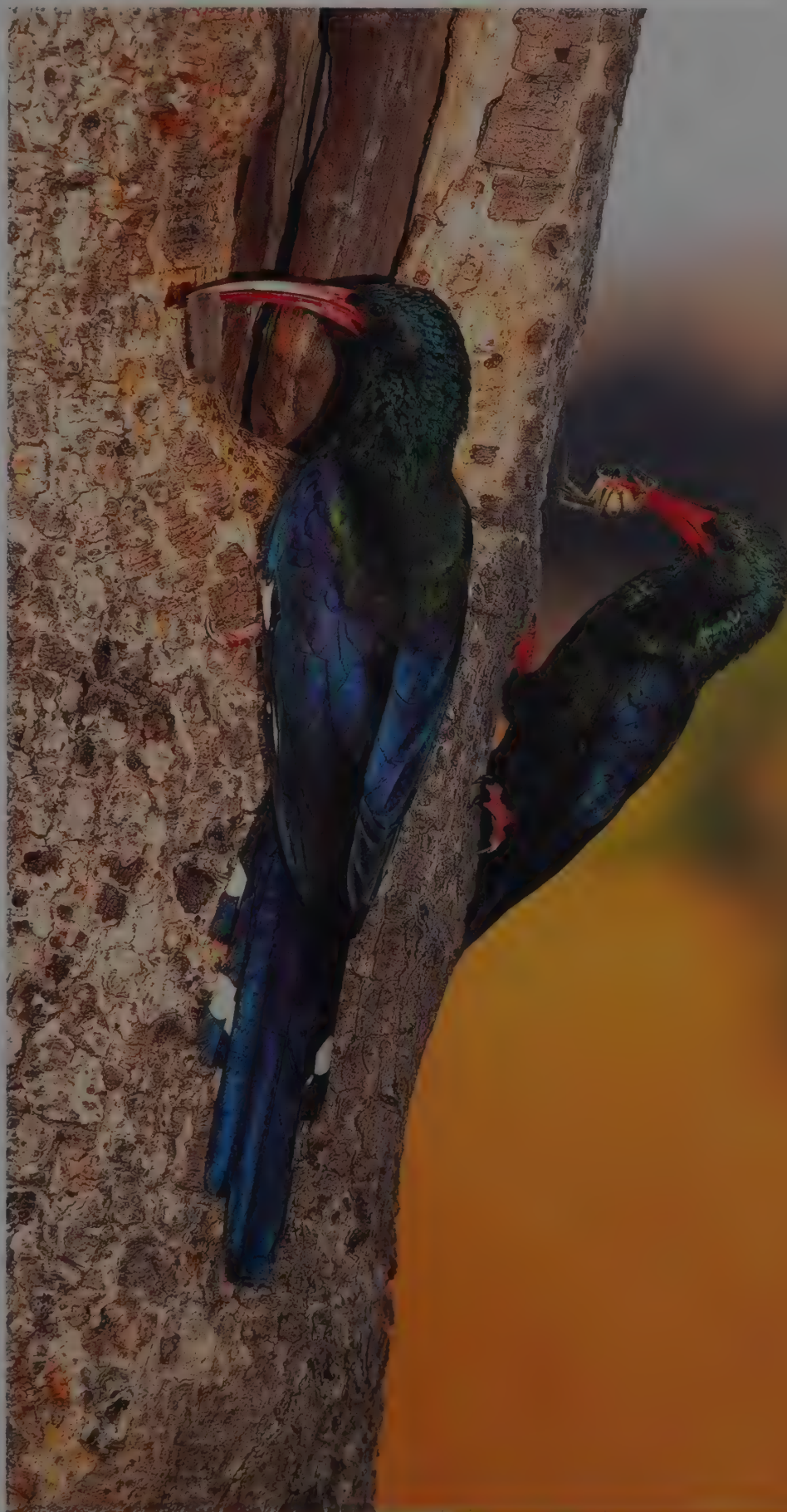
All members of the Phoeniculidae feed primarily on arthropods. In addition to both larval and adult insects of a variety of orders, they consume spiders, solifugids, millipedes and centipedes, as well as the egg masses of insects and spiders. In West Africa, small lizards are taken by Green Woodhoopoes, and eggs of small birds are eaten by the Violet Woodhoopoe. At least six of the eight species of phoeniculid have been reported to eat berries and seeds, in addition to animal prey. This has usually been determined by examination of stomach contents of collected specimens, and the plants involved have apparently rarely been identified.

While all woodhoopoes are distinctly arboreal, spending most of the day foraging in trees, at least some species are highly flexible in their foraging behaviour. For example, when termites are swarming, Green Woodhoopoes become effective aerial insectivores, and occasionally individuals of this species develop completely novel forms of foraging. Despite their specialized bill morphology and foraging behaviour, some, and perhaps all, phoeniculids retain the ability to respond opportunistically to unusual situations. Even the Common Scimitarbill, with its extraordinarily specialized bill, has been recorded foraging on the ground, a habit also indulged in, albeit rarely, by Green Woodhoopoes. On such occasions, these birds hop, unlike their terrestrial relatives the hoopoes, which walk across the ground. In Kenya, Green Woodhoopoes have been observed tearing apart cowpats to obtain the small beetles residing therein. Interestingly, in South Africa, two members of a Green Woodhoopoe flock learned to take food items from the mouths or throats of nestlings of other species immediately after the chicks had been fed. In both of these cases, the novel behaviour was recorded from only one flock of woodhoopoes, but, within that social unit, it was recorded from that same flock even after the individuals which initially exhibited such behaviour had disappeared. This



About to provision nestlings, two spectacularly iridescent Green Woodhoopoes have arrived at the nest cavity with food. The longer-billed male on the left carries a larval insect, whereas the shorter-billed female has captured a spider. Differences in bill size between the sexes have been linked with corresponding differences in foraging behaviour, the males tending to feed lower down on the trunks of trees and on larger branches, and the females preferring to feed higher on the trunk and on smaller branches. The short legs and strong claws, and the long, graduated tail, obvious adaptations for clinging to tree trunks, are readily apparent in the female and male, respectively. In addition to probing crevices, Green Woodhoopoes may use the strong bill to hammer flakes of bark from tree trunks in their search for arthropods. Prey items are often subdued by slamming against a branch, being literally beaten into submission! This species also forages on the ground at times, especially males, and both sexes become effective aerial insectivores during termite swarms. Whether the two birds shown here are the parents of the young inside the cavity is an open question, because groups of 4-8 birds, and sometimes larger numbers, co-operate in bringing food items to the nest, although only the two breeding adults contribute genetically to the brood.

[*Phoeniculus purpureus*,  
Zimbabwe.  
Photo: R. Peek/Aquila]





suggests that the behaviour not only was originally learnt, but also was passed on, presumably by observational learning, to other flock-members.

At Lake Naivasha, in Kenya, large numbers of caterpillars of the genus *Cossus* occasionally appear simultaneously on the surface of the ground at the base of a large yellow-barked acacia (*Acacia xanthophloea*). Although these caterpillars appear to be aposematically coloured, being bright orange, they are avidly devoured by Green Woodhoopoes, Grey-backed Fiscals (*Lanius excubitoroides*), African Grey Hornbills (*Tockus nasutus*) and Superb Starlings (*Lamprolornis superbus*). In view of the responses of these birds to them, the adaptive significance of the mass appearances of these colourful caterpillars during daylight hours is far from obvious!

Despite the capacity to take advantage of unusual foraging opportunities, however, this family's foraging behaviour is typically rather specialized. All species are highly arboreal, and all use the bill to probe into crevices and cracks in and under the bark, as well as to glean insects from small terminal branches and twigs. The behaviour of Green Woodhoopoes has been closely studied at Lake Naivasha. At this site, it appeared that the typical method of foraging was distinctively different from that of all other birds in the area, and that this allowed the woodhoopoes to obtain prey items that were inaccessible to other avian species. For example, following the long rains, these birds feed themselves and their young primarily on caterpillars. The caterpillars forage at night and retire to hiding places during the day, thus avoiding most avian predators. Although numerous other kinds of bird, such as cuckoo-shrikes (*Coracina*), also feed on these same insects, they are unable to reach the crevices and cracks on the undersides of limbs and branches that often hold several caterpillars. It appears that the ability of the woodhoopoes to obtain food from sites that are essentially unavailable to other insectivorous species has been a critical factor in the success of phoeniculids compared with other non-passerine insectivores, and even with many insectivorous passerines as well. In prime habitat for lepidopteran larvae, such as open yellow-barked acacia woodland in Kenya, densities of Green Woodhoopoes can be surprisingly high.

The woodhoopoes' ability to obtain food from sources largely unavailable to other species is reflected in their morphology, as well as their behaviour, both of which are specialized for foraging on the trunks, limbs and smaller branches of trees. The most obvious foraging adaptation is the bill, which, to varying degrees, is shaped rather like curved forceps. As their common names suggest, the most extreme development of the bill along these lines is seen in the two scimitarbills. The Forest Woodhoopoe, possibly the most primitive living member of the group (see Systematics), possesses the least specialized bill shape. Less conspicuous than the bill, but no less important to the special foraging abilities of the members of this group, are the legs and feet. The tarsi are quite short and thick, and the feet, or, more accurately, the toes, are very strong, with long, sharply curved claws. These traits enable the bird to hold itself in place as it forages perpendicular to the trunk or branch of a tree, and even allow it to hang on to the underside of a horizontal branch, or to hang upside-down. The Common Scimitarbill is capable of moving down tree trunks with the head pointed downwards. The third structure that appears to be especially important in foraging is the elongated tail, which is used as a prop as the bird moves up the trunks and branches of trees. This use of the long tail as a brace leads to abrasion of the rectrices, and woodhoopoes often exhibit a badly worn tail. It is the combination of the long forceps-like bill and the specialized legs and toes, and, to a lesser extent, the tail, that gives phoeniculids their apparently unique ability to search out crevices and cracks that apparently are inaccessible to other arboreal sympatric avian insectivores; in other words, these traits have made possible the unique foraging niche of the woodhoopoes.

It is interesting to speculate that the white head of the White-headed Woodhoopoe and of one subspecies of the Forest Woodhoopoe has evolved as an adaptation to aid in peering into crevices and cracks, in areas where light is limited. Light reflected from the white head may serve to enhance the bird's abil-

ity to see into dark cracks and similar places. Consistent with this speculative suggestion is the fact that both of these woodhoopoes typically inhabit deeply shaded primary forest, in contrast to the other species in this group. Similar explanations have been offered for the white coloration of the White-headed Woodpecker (*Picoides albolarvatus*) and the White-breasted Nuthatch (*Sitta carolinensis*) in North America.

At Lake Naivasha, in years in which the temporal pattern and the amount of rainfall are normal, lepidopteran caterpillars make up over 90% of the food brought to nestling Green Woodhoopoes. During the breeding season, these birds are caterpillar specialists. Rainfall in this region is markedly seasonal, and the climate is typically very dry from December to April. During this dry period, caterpillars become increasingly more scarce; correspondingly, the diets and foraging patterns of the birds become more variable, and the birds often appear to be hard pressed to obtain sufficient food to maintain their condition. For example, individuals spend a lot of time searching for minute food items by tearing apart wads of debris, such as dried acacia leaves, held together by spider webs. Uncommonly, groups leave their year-round territories at this time to forage in isolated groves of trees that apparently are outside the boundaries of the territories of other woodhoopoe flocks. There is probably seasonal variation in food availability in other parts of this species' range, as well. In South Africa, mortality of adults is significantly higher during the winter than during the summer, and du Plessis and Williams have attributed this to seasonal differences in overall energy balance.

Male and female Green Woodhoopoes differ considerably in body mass and in bill length (see Morphological Aspects). Corresponding to these morphological differences, males and females tend to forage in different parts of the trees. Thus, females forage more on small terminal branches and twigs, whereas males, in contrast, frequently feed on the main trunk and large branches, as well as on the ground at the bases of the acacia trees.

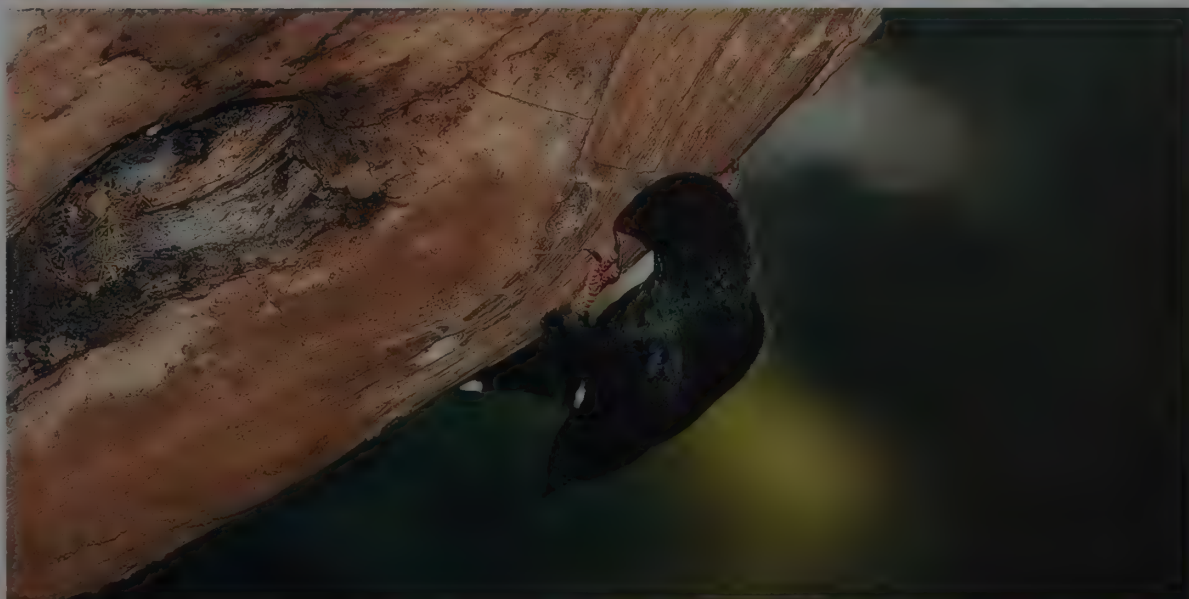
The Forest Woodhoopoe and the Common Scimitarbill have been reported to participate in mixed-species foraging flocks. In Zambia, the Common Scimitarbill was recorded in about 22% of such groupings; the three most frequent members of these parties were the Fork-tailed Drongo (*Dicrurus adsimilis*), the Chinspot Batis (*Batis molitor*) and the Black-backed Puffback (*Dryoscopus cubla*). The species foraging with Forest Woodhoopoes have not, apparently, been recorded.

## Breeding

Although the nest-sites and eggs have been described for all members of the Phoeniculidae except the Forest Woodhoopoe, little more is known about the breeding habits of most species. So far as is known, all species typically nest in cavities in trees, which may either be natural hollows or be holes excavated by woodpeckers or barbets (Capitonidae).

The available information suggests that a conspicuous component of breeding behaviour within the family falls into two categories along generic lines. All three members of the genus *Rhinopomastus* apparently show the most typical avian pattern of parental care, with only a single male and a single female participating in the rearing of the young. In contrast, it appears likely that all of the *Phoeniculus* species except for, possibly, the Forest Woodhoopoe, the social and breeding systems of which are unknown, engage in co-operative breeding. Co-operative breeding is characterized by the presence of both breeding and mature non-breeding individuals in a social unit or flock (see General Habits); the non-breeders are usually referred to as "helpers". Helpers contribute to the reproductive effort by feeding the chicks and otherwise caring for them. Co-operative breeding in one species, the Green Woodhoopoe, has received detailed study in Kenya and South Africa. Like the Green Woodhoopoe, the White-headed Woodhoopoe occurs in permanent flocks and breeds co-operatively. Limited data suggest that Black-billed and Violet Woodhoopoes also live in permanent and presumably co-operatively breeding groups.





In addition to gleaning prey items from the surface of the foraging substrate, phoeniculids use their curved bill to probe into cracks in much the same manner as a wader (Scolopacidae), the main difference, of course, being that the hole is usually in the trunk or branch of a tree, rather than on a mudflat. Here, a Green Woodhoopoe investigates a small hole in a tree trunk, literally probing to the full length of its bill. One might think that a long tongue would be beneficial in this situation, but phoeniculids have a rather short tongue. This is in marked contrast to the extremely long tongues of many woodpeckers (Picidae) that enable them to extract prey items from holes in trees. The difference in tongue morphology between the two families underscores the fact that woodhoopoes and scimitarbills have a much more diverse suite of foraging behaviour than do woodpeckers, and a tongue specialized for prizing food items from holes would probably be maladaptive for many of the other foraging manoeuvres used by phoeniculids. Moreover, the thin bill of phoeniculids is probably better for grasping prey than is the chisel-like bill of woodpeckers.

[*Phoeniculus purpureus marwizi*,  
Samburu Game  
Reserve, Kenya.  
Photos: Denis Huot/Bios]

In tropical Africa, it appears that breeding by the various phoeniculid species may occur over much of the year, and that considerable variation exists from year to year both in the onset of breeding and in how many pairs in a local population attempt to breed. In Ghana, in West Africa, eggs and/or young have been recorded for the Green Woodhoopoe during every month of the year. Similarly, at Lake Naivasha in Kenya, in one year or another, some pairs or groups of Green Woodhoopoes began nesting in nearly all months from May to January, the most predictable pattern being widespread initiation of breeding in June, following the "long rains" of April and May. At Naivasha, year-to-year variation in nesting attempts was clearly related to the pattern and amount of rainfall. Interestingly, in one year, heavy rains during what is usually the dry season, in December-February, subsequently led to greatly decreased reproductive effort; the wetness of the ground, during a period of time when it would normally have been very dry, apparently led to high mortality of the lepidopteran larvae pupating in the soil. In contrast, in South Africa, the breeding season of the Green Woodhoopoe is more restricted, with nesting activities usually being initiated only from September to November. More limited information for most other species of phoeniculid also suggests a flexible temporal pattern of breeding.

In Kenya, if environmental conditions are ideal, a pair of Green Woodhoopoes sometimes produces up to three broods in a calendar-year; such optimal conditions, however, rarely occur. In South Africa, where the breeding season is temporally restricted, only one brood per year is produced. The frequency of breeding by individual pairs is entirely unknown for other species of phoeniculid.

It appears that all phoeniculids, including the co-operatively breeding ones, are monogamous. No instances of extra-pair fertilizations have yet been reported for any species. In the Green Woodhoopoe, prior to actual nesting, the breeding pair leaves the rest of the group one or more times each day, and spends a considerable amount of time perched quietly in or near the chosen nest tree, engaged in mutual grooming and periodic copulation. In addition, before egg-laying, the breeding female begins to solicit food from all flock-members by uttering a particular vocalization, an intense "twittering". The provisioning of the female by her mate and other flock-members at this time probably serves two important functions: first, it promotes rapid weight gain by the female, mostly via enlargement of the reproductive tract, and thus supports egg production; and, secondly, it may serve to "train" non-breeding flock-members, especially younger ones, to respond to the female's solicitation, which will later be important in the



*Despite the flexibility in foraging behaviour shown by Green Woodhoopoes, during the breeding season they often specialize on lepidopteran larvae. This individual, almost surely a male judging by the size of its bill, has captured a plump caterpillar. Studies at Lake Naivasha, Kenya, have shown that the morphology and foraging behaviour of Green Woodhoopoes allow them to catch large numbers of caterpillars that forage in the open at night and hide in deep crevices and beneath bark by day, seeking refuge in places that are largely inaccessible to the rest of the local avifauna. In this manner, the woodhoopoes have effectively eliminated any inter-specific competition that might otherwise have arisen for these food items. As further evidence of the amazing foraging abilities of these birds, two Green Woodhoopoes from a flock in South Africa learned to steal food from the mouths of nestlings of other bird species right after the parents had delivered the morsels. This novel feeding behaviour was observed in the same flock after the original participants had disappeared, suggesting that the behaviour was culturally transmitted among flock members.*

[*Phoeniculus purpureus*, Zimbabwe.  
Photo: R. Peek/Aquila]





Although all phoeniculids are primarily arboreal feeders, most species, except perhaps the Forest Woodhoopoe (*Phoeniculus castaneiceps*) and the White-headed Woodhoopoe (*P. bollei*), forage on the ground from time to time, as demonstrated by this Common Scimitarbill. When feeding on the ground, woodhoopes and scimitarbills hop rather than stride, which distinguishes them from their close relatives, the largely terrestrial hoopoes (*Upupidae*).

[*Rhinopomastus cyanomelas cyanomelas*, South Africa.  
Photo: Roland Seitre/Bios]

provisioning of nestlings. It is interesting that the female Common Scimitarbill, a species which is not a co-operative breeder, apparently solicits food from her mate by the use of similar vocalizations to that described for the Green Woodhoopoe.

As with most other hole-nesting species, these birds are often constrained in their choice of nesting location. The nests of the Green Woodhoopoe are often in sites that appear to be highly vulnerable to predation, and many nests fail as a result of predators. It appears that the female chooses the nest-cavity partly on the basis of its proximity to areas rich in food, and that this may account for the great variation in the quality of successive cavities used by an individual female. Before actual nesting begins, a female may, over a period of several days, enter several cavities located at different sites within the territory, and give the "twittering" call for food from each of them. The amount or quality of the food delivered by her mate and other flock-members to each prospective nest-site may determine which site is eventually chosen. Behaviour related to nest-site selection is unreported for other members of the family.

Notwithstanding the fact that the phoeniculids typically lay their eggs in hollows in living or dead trees, there are several recorded instances of other sites being used. In Kenya, the nest of a group of Green Woodhoopes was located in a slight depression immediately on the ground, underneath a piece of farm machinery parked in an open shed. Other nests of this species have been placed in similarly unlikely sites: for example, in Ghana, nests have been found in the roofs of houses and in the wooden mounting of an air conditioner. The use of such atypical nest-sites testifies both to the behavioural flexibility of the Green Woodhoopoe and to the difficulty in some cases of locating or obtaining suitable tree cavities for nesting.

Although Green Woodhoopes sometimes remove nest material placed in cavities by other species, they do not engage in any form of nest construction. The Common Scimitarbill, on the other hand, does bring some nest material, such as lichens or dead leaves, to the nest-cavity. This may represent the evolutionary remnants of nest-building behaviour of an ancestral phoeniculid. When one also considers the egg colour of these birds, described below, this speculative interpretation is rendered more likely than the alternative, namely that it represents an early stage in the ongoing evolution of nest-building.

Unlike those of many families of birds that are obligate cavity-nesters, the eggs of phoeniculids are not white. Rather, they range in colour from blue to turquoise to grey or olive-green, usually with small, white chalky pits. The eggs of the White-headed Woodhoopoe are also covered with spots and blotches of chocolate-brown. In the scimitarbills, the eggs also show chalky pits on the surface. Although rare among hole-nesting birds, this kind of egg colour is common in cup-nesting species, and is thought to provide camouflage when eggs are laid in open nests situated in leafy vegetation. Thus, egg colour, together with the collection of nest material by at least one species, the Common Scimitarbill, suggests the possibility that open cup-nests occurred at some point in the ancestry of this group. The eggs are elliptical in shape, and range in average size from  $26 \times 18$  mm in the case of the Black-billed Woodhoopoe to about  $21 \times 15$  mm in the Abyssinian Scimitarbill.

For some species, data on clutch size are minimal or non-existent. Green Woodhoopes in Kenya lay at the rate of one egg per day, and clutch size ranges from two to five eggs, with an average of 3.35; the vast majority of 60 clutches numbered three or four eggs. In South Africa, the average for 13 clutches was almost one egg less, at 2.54. The very few data available indicate that other *Phoeniculus* species produce clutches of similar size. Clutch size may average slightly smaller in the species of *Rhinopomastus*, though the data currently available are probably too scant for firm conclusions.

In the Green Woodhoopoe, incubation is conducted solely by the breeding female, which remains in or near the nest most of the time and is fed by her mate and by non-breeding flock-members. Limited data suggest that female Common Scimitarbills also carry out all incubation, and that they are fed extensively by the male. This is likely, therefore, to be the pattern for all members of the family. For the Green Woodhoopoe, the incubation period is 17-18 days. At 21 nests of this species near Lake Naivasha, observed during incubation for a total of 335 hours, the female breeder was fed an average of about 5.5 times per hour by her mate and helpers.

At hatching, Green Woodhoopoe chicks weigh 2.5-3 g. They have long white down growing from the feather tracts, their heel pads and commissural points are well developed, and the lower mandible is longer than the upper. Apart from their ability to

raise the head to receive food, newly hatched chicks are completely helpless. Starvation of hatchlings is rare, this being possibly related to the fact that only part of the clutch hatches (see below), and growth, especially during the first half of the nestling stage, is rapid. The young birds are well developed by the time they fledge, at 28-30 days of age. Increase in mass continues, however, for some time after fledging.

Once the chicks of the Green Woodhoopoe begin to hatch, the male breeder and experienced helpers soon start to arrive at the nest with very small food items. At this time all food is passed on to the female parent, and she delivers it to the chicks. Inexperienced helpers, especially males, may arrive with inappropriately large food items, which the female parent then eats. For about the first two weeks of nestling life, virtually all food brought to the nest is transferred to the female breeder, rather than being delivered directly to the chicks. After that period, helpers, especially females, begin to avoid the female breeder and to enter the nest to feed the chicks directly. From the beginning, female helpers appear to be more attuned to the nestlings' needs in that they are more likely than males to provide the very small food items required by newly hatched chicks. As a rule, therefore, when a group contains helpers of both sexes, it is the female helpers that first begin to enter the nest-cavity and interact directly with the nestlings, sometimes remaining in the nest for extended periods of time. Male helpers may begin to feed the chicks directly only after the latter are capable of climbing to the nest entrance.

The faeces of nestling woodhoopoes are not removed by the parents and helpers, and this fact has given woodhoopoe nests a reputation for being filthy. As the young develop, however, they come to defecate at one spot within the nest-cavity, rather than doing so indiscriminately, and this habit usually makes it possible for the feathers and feet of the young birds to remain clean. If the weather is dry, accumulated fecal matter does not appear to pose a problem, but during rainy periods, if moisture seeps into the cavity, the floor of the nest can indeed become fetid. To add to the putrid smells coming from the nest itself, the young woodhoopoes, if frightened, expel from the anus an extremely smelly liquid, while at the same time secreting a strongly odorous substance from the oil-gland (see General Habits).

Although Green Woodhoopoe helpers provide much of the food brought to the nestlings, they appear to have little or no effect on the number of chicks fledged per nest or per year. This pattern holds true both in Kenya, where two or three broods may be produced in a single year, and in South Africa, where nesting occurs only once per year. For the other group-living species of phoeniculid, the effects, if any, of helpers on productivity are unknown.

With regard to helping or "alloparental" behaviour and kinship ties, experimental studies of Green Woodhoopoes conducted in South Africa have shown that adult birds do not discriminate between their own chicks and "foreign" ones when both are present in the nest. In fact, Green Woodhoopoes even occasionally feed nestlings of the Crowned Hornbill (*Tockus alboterminatus*), as well as regularly rearing chicks of the socially parasitic Greater Honeyguide (*Indicator indicator*). Furthermore, they do not preferentially feed chicks in the original nest as opposed to those in an experimental nest placed nearby. This is true of both breeders and helpers. In addition, in both South Africa and Kenya, recent immigrants into woodhoopoe flocks provide nestlings with as much food as do other, established non-breeding group-members. Thus, it appears that alloparental feeding behaviour is not related to nest-site specificity, kin discrimination or prior association with breeders. For most co-operatively breeding species, helpers have been shown to gain some sort of benefit or "repayment" as a result of their aid to chicks. Such repayment can be either an "indirect" benefit, in the form of the genes shared between helper and chick, or a "direct" one, in the form of some kind of positive benefit to the helper. In Kenya, helpers often gain some direct benefits from the social bonds they form with the chicks which they have helped to rear, these taking the form of alliances that promote the interests of the former helper. In contrast, in South Africa, no fitness benefits to helpers, either direct or indirect, were detected as a result of their feeding contributions to young birds. In this case, it has been suggested

that the vocal and visual stimuli provided by nestling Green Woodhoopoes elicit unmodified parental feeding behaviour; in other words, helping behaviour is simply a manifestation of the evolved parental response, released by the sound and sight of nestlings.

As soon as the chicks fledge, they begin to move with, and are cared for by, the entire flock. In addition to providing food, flock-members protect the young birds by providing aerial escort as they fly from tree to tree. Various flock-members also guide the naive juveniles by the use of conspicuous, exaggerated wingstrokes as they fly with or ahead of them. Helpers also participate in leading the young to a roost-cavity and enticing them to enter it. Parents and helpers may then feed the young birds; this appears to encourage them to remain within the cavity, even though the rest of the flock may continue to forage nearby for quite some time. The integrated, co-operative nature of a social unit of Green Woodhoopoes is perhaps most conspicuous when the entire group is occupied with caring for and protecting newly fledged juveniles. All flock-members move with the young fledglings each time they fly, providing protection from aerial predators such as the Gabar Goshawk (*Micronisus gabar*). The young birds continue to be fed and protected by adult flock-members for several weeks after fledging.

Limited observations on chick care have been recorded also for other species. In the Common Scimitarbill, as in the Green Woodhoopoe, the female remains in the nest with small chicks while her mate procures and delivers food, which she relays to the chicks. Similarly, in the Black Woodhoopoe, the female may enter the nest to receive food brought by the male, and then deliver it to the nestlings. It seems probable that the division of parental duties is similar for all phoeniculids: the female alone carries out all incubation, and she provides virtually all the direct parental care to small nestlings.

One of the most interesting and puzzling aspects of the breeding biology of Green Woodhoopoes in Kenya is the regular failure of one or more eggs to hatch. Of a sample of 200 eggs from 60 nests, only 127 (64%) hatched; at least one egg failed to hatch in 82% of the 60 nests. Two alternative interpretations of this high frequency of unhatched eggs have been offered by J. D. and S. H. Ligon, one adaptive and one non-adaptive.

An adaptive explanation is based on the finding that, under certain conditions, the sex ratio of broods of young is significantly biased towards female chicks. In a population of Green Woodhoopoes in Kenya, there was a female-biased sex ratio in first nests of the year among those female breeders that had two, one or no helpers. Apart from occasional instances of predation of entire broods, nestling mortality was extremely low, at only 5%; thus, this bias was not based on differential starvation of male and female chicks. When helpers are few, production of female offspring by breeders in small groups may be adaptive, in that females are smaller and are probably less expensive to rear than males. Young female helpers also contributed significantly more feedings to subsequent broods than did their male siblings of the same age. The bias towards daughters could be effected either through non-random segregation of sex chromosomes or by differential mortality of eggs according to sex. Embryonic mortality is high in this population, with most clutches having at least one egg that fails to hatch. Studies of several other bird species suggest that larger eggs may give rise to males, which provides a possible means for the female parent to discriminate the sex of offspring prior to hatching.

The non-adaptive interpretation of hatching failure is based on the phenomenon of inbreeding depression. The Green Woodhoopoes studied in Kenya are extremely philopatric (see Movements), which leads to neighbourhoods of territories that contain close relatives. Many breeding birds in neighbouring territories either were parents and offspring or were siblings. Under these circumstances, many of the young birds produced by these breeders were related, at minimum, at the first-cousin level. This situation inevitably results in some breeding pairs being made up of related individuals, such as a nephew and an aunt. It also leads to the conclusion that the woodhoopoe population overall may be inbred. Although related birds do sometimes form pair-bonds, it appears that close relatives in the same



Thanks to intensive studies of marked individuals, vastly more is known about the breeding habits of the Green Woodhoopoe than of any other phoeniculid. The breeding pair may be attended by as many as 14 helpers that work together to feed the incubating female, raise the young, watch for predators, defend the territory from conspecifics, and perform other duties that in most species are routinely undertaken only by the parents of the brood. This bird has brought a tiny food item to the nest, which suggests that the young are probably less than two weeks old.

The typical nest is a natural cavity, such as the one depicted here, or an old hole made by a barbet (Capitonidae) or a woodpecker (Picidae). Atypical nests have been found on the ground beneath farm machinery and in human-made sites, such as barns and an old air-conditioner! So far as is known, helpers do not contribute genetically to the broods they assist, and they tend to be offspring or siblings of one or both of the breeders. Interestingly, no clear relationship exists between the number of helpers in a group and the number of young produced, raising the question of why helpers "help" in the first place. The evidence suggests that woodhoopoe helpers benefit by increasing their chances of inheriting a breeding slot on the territory in which they help. Thus, rather than being an altruistic behaviour, or one that evolves because of kin selection, helping in Green Woodhoopoes appears to be tied to potential direct benefits to helpers.

[*Phoeniculus purpureus angolensis*,  
Okavango Delta,  
Botswana.

Photo: Pete Oxford/  
BBC Natural History Unit]





flock, such as parents and their offspring, or brothers and sisters, never mate.

Both the high frequency of nests producing unhatched eggs (82%) and the fact that most of the unhatched eggs examined contained embryos that had died at various stages of development up to the point of hatching are suggestive of inbreeding depression. If this interpretation is correct, it appears that this situation is due to the following factors. First, because Lake Naivasha is largely surrounded by the open grassland of the Rift Valley, the Green Woodhoopoe population there is somewhat isolated. Secondly, the breeding population is not large, having been estimated to contain about 105 breeding pairs of birds, plus their helpers. Thirdly, these birds are, as already mentioned, extremely philopatric, this philopatry being due probably to the large costs of long-distance dispersal (see Movements). Thus, a young woodhoopoe may have the option either to disperse a long distance, with the attendant risks, and thereby avoid mating with a relative, or to disperse a short distance, or not at all, and then accept the costs associated with inbreeding, such as reduced hatchability of eggs. The latter is the pattern shown by these birds, possibly because the cost of inbreeding, as manifested by reduced hatching rate, may not be very significant to the lifetime reproductive success of an individual Green Woodhoopoe. There are two reasons for this: starvation of nestlings is almost non-existent, perhaps as a result of the reduced brood size brought about by inbreeding; and the reproductive potential of birds that have attained breeding status is high, with the possibility of up to three broods per year.

Lifetime reproductive success of Green Woodhoopoes has been studied in Kenya. The most important factor influencing this success is the quality of the territory on which a pair of birds breeds. Year in and year out, certain territories consistently either produce more woodhoopoes than are lost or produce fewer than are lost. With regard to annual natality and annual mortality, territories fell into two distinct categories. Either they were very productive, or they were virtually non-productive. There were no intermediate values, so that, in this case, "average" productivity of all territories does not reflect the actual situation. Over a period of a decade, the original breeders in the best territories had left 13-18 descendants on the study site. In contrast, in the others, the original breeders had either no descendants or, in one case, a single descendant. In these latter territories, flocks persisted over time only as the result of immigration of new birds from elsewhere. The factors most important in determining the relative productivity of territories appear to be the number and quality of roost-sites, which correlate with the number and size of the trees within the territory; at the Kenyan study site, nearly all trees were of a single species, the yellow-barked acacia. These factors are related because large trees are more likely than small ones to hold cavities suitable for roosting and nesting. In addition, Green Woodhoopoes prefer to forage in larger trees, probably because they are richer in the arthropod foods taken by this species.

## Movements

No information about movements is available for most species and populations of phoeniculid. Green Woodhoopoes at Lake Naivasha, in Kenya, where almost 400 individuals were ringed for individual recognition over the course of several years, are highly sedentary. Many of the birds ringed as juveniles eventually obtained breeding status either within their natal territory or in a nearby territory. At this site, the eventual breeding location was determined for 38 female and 33 male Green Woodhoopoes ringed as juveniles. Of these, 18 females and nine males bred in their natal territories. Of the woodhoopoes that did disperse, 20 males and 14 females became breeders in a territory adjacent to the one in which they were hatched. The remaining four males bred only two territories away from their parental territory, while five of the remaining six females bred from two to six territories away; the sixth female is known to have moved considerably farther, an estimated 13 territories away. In short, this population of Green Woodhoopoes is extremely philopatric. Similar limited

dispersal has been recorded for this species in South Africa by du Plessis. At two study sites, many individuals obtained breeding status in their natal territory, and, when birds did disperse, they travelled no farther than six and four territories, respectively.

In Kenya, Green Woodhoopoes usually emigrate to a new territory in a "team" of two or more individuals of the same sex (see General Habits). Such movements are not predictable. Rather, they are triggered by a vacancy in a nearby territory resulting from the disappearance of previous occupants of one sex or the other; emigration from one territory to another may, therefore, occur at any time during the annual cycle. This appears to be based on intra-sexual competition for territorial vacancies. There is strength in numbers, and even two birds are far more likely to obtain entry into a new territory than is a lone individual. Such movement typically involves a former helper and one or more younger birds that it had helped to rear. Helpers gaining a breeding position in a new territory are thus "repaid" for the aid they have previously given to younger flockmates of the same sex. In contrast, Green Woodhoopoes in South Africa do not exhibit group emigration; instead, single individuals of both sexes engage in "scouting forays", in which they search for a territorial vacancy.

The conservative dispersal patterns shown by Green Woodhoopoes in both Kenya and South Africa are unusual, since many kinds of birds, including most co-operatively breeding species, exhibit a difference between the sexes in dispersal patterns and distances, with females being the "dispersing sex". As described above, female Green Woodhoopoes do not follow this rule. The fact that more females than males breed in the territory in which they were hatched may be unique among the co-operatively breeding birds studied to date.

The extreme philopatry shown by both female and male Green Woodhoopoes, usually moving no farther than to an adjacent territory, is probably related to their dependence on cavities for roosting. Woodhoopoes occupy very large territories, and flocks commonly intrude into neighbouring territories when the rightful owners are elsewhere. A conspicuous aspect of the behaviour of an intruding flock is exploration of the owners' roost-cavities and other tree holes within the territory. As a result of this kind of behaviour, an individual woodhoopoe presumably learns the location and quality of cavities in surrounding territories. This information may be essential to a bird's decision whether or not to move into a nearby territory when the opportunity arises. Variation in territory quality, based on the quantity and quality of available and potential roost-sites, probably determines in large part whether woodhoopoes will emigrate to a nearby territory when a breeding vacancy becomes available.

Although Green Woodhoopoes are extremely sedentary throughout the year in Kenya and South Africa, this may not be the case over the entire geographical range of this widespread species. In Chad, these woodhoopoes are said to move north into drier savanna during the wet season.

One other phoeniculid species may also exhibit similar seasonal movements in West Africa. In Nigeria, and possibly elsewhere, it appears that the Black Woodhoopoe may, like the Green Woodhoopoe in Chad, range north into drier habitats during the wet season and withdraw south during the dry season.

## Relationship with Man

Any influences that woodhoopoes may have, or have had, on human populations in the areas in which the two live together are difficult to discover. Although these birds are not particularly well known, it would seem likely that their hole-nesting and hole-roosting habits would lead to some superstitious beliefs in the minds of local people. Birds which live in smelly holes in trees often evoke superstitions and ideas of associated unpleasantness or even "badness", but, if any such beliefs relate to the woodhoopoes, they appear to be unknown to outside observers.

By far the best-known member of the family, the Green Woodhoopoe is not particularly wary or shy of people. This species often nests in gardens and other areas in which human ac-





These Green Woodhoopoe nestlings probably represent the entire annual production for the pair inhabiting this territory in South Africa. Mean clutch size is 2-3 eggs, and only one brood is attempted per year in the short breeding season at this latitude. Mean clutch size is 3-4 eggs in tropical Kenya, and two or even three broods may be raised in good years. Nests often fail due to predation by genets (*Genetta*), which also inflict high mortality on adults, and from brood parasitism by Greater Honeyguides (Indicator indicator). When the young are too small to climb to the nest entrance, helpers pass food to the brooding female, but when they are old enough to appear at the nest entrance, helpers feed them directly.

[*Phoeniculus purpureus*, Nylsvley, South Africa. Photo: Warwick Tarboton]

tivity is common. Because these birds are noisy and often conduct their activities in the proximity of people, they do sometimes draw the attention of humans. Some names of African peoples for the Green Woodhoopoe are based on its vocalizations. The prolonged cackling or chuckling sounds made by a flock in a rally display (see General Habits, Voice) have given rise to the Afrikaans name *kakelaar*, meaning "cackler", while the same vocalization has led to this species being referred to in the Xhosa and Zulu languages by the highly evocative name of *hlekabafazi*, which translates as "the hysterical laughter of women".

Other species of this group are less conspicuous than the Green Woodhoopoe and its close relatives, the Black-billed and Violet Woodhoopoes. Indeed, the Forest Woodhoopoe and the three *Rhinopomastus* species probably usually go largely unnoticed by people.

The relationship of man and the members of the family Phoeniculidae are largely incidental to other human activities, in particular habitat destruction (see Status and Conservation).

### Status and Conservation

At present, there is no reason to think that any of the eight species of phoeniculid is faced with outright extinction within the near future. The most likely threat to the continued existence of some species is habitat destruction. The explosive increase of human populations in tropical Africa, along with social unrest, which can make it difficult or impossible to census birds and other animals, does not bode well for the future of, especially, forest-inhabiting species of wildlife. Thus, the rapidly growing human population, with its associated destruction of habitat, poses the most serious threat to African wildlife.

With regard to phoeniculids, in particular, the two equatorial, forest-dwelling species, the Forest Woodhoopoe and the White-headed Woodhoopoe, are likely eventually to become threatened or even endangered over much of their respective ranges as a result of loss of their forest habitat. Indeed, this has already occurred at the eastern edge of the range of the Forest Woodhoopoe in western Kenya, where this species appears to have been extirpated, probably as a direct result of habitat destruction.

In contrast, several other species, such as the Green and Black Woodhoopoes and the Common Scimitarbill, occur over vast areas, over much of sub-Saharan Africa. Because these species are so extremely widespread, it appears unlikely that any of them will be faced with extinction within the foreseeable future. The prospects for others, such as the Abyssinian Scimitarbill, are more difficult to predict. This species has a much smaller total range in arid semi-desert bush country, where one might expect the harsh climatic conditions to make it improbable that the environment would be strongly modified by humans in the near future. On the other hand, the cutting of the relatively few large trees in such areas, for charcoal or for any other reason, could have a great impact on these and other cavity-dependent birds by removing potential sites for nesting and roosting. Such large trees are both scarce and slow-growing, and their removal would therefore have a major adverse effect both at the current time and well into the future. The same concern could be raised for the arid-country Black-billed Woodhoopoe.

Another problem that is conspicuous in Kenya, and one that is also present in other African countries, is the felling of native tree species and replacing them, if they are replaced at all, with exotics such as eucalyptus or pepper trees. If reforestation efforts, when they are made, focused instead on native tree species rather than exotics, this would go some way towards repairing the original damage to the native woodland and its occupants, avian and otherwise.

In addition to the intentional cutting of woodland, inadvertent habitat destruction occurs in protected parks and reserves, at least in part as a result of human-induced factors. In Amboseli National Park, in southern Kenya, the *Acacia* woodland has been damaged by salt in rising groundwater levels, and also by elephants, which are largely confined to the park because of the dangers to them were they to leave the protected area. Thus, within this world-famous national park, the *Acacia*-woodland habitat of species such as the Common Scimitarbill and Green Woodhoopoe, not to mention other arboreal birds and other animals, is seriously threatened.

One particular example, again from Kenya, may serve to illustrate the seriousness of the threat posed by habitat destruction to woodhoopoes and other kinds of bird, and the difficulties of combating such major problems. On a large, privately owned farm near Lake Naivasha, the park-like or savanna-like woodland composed almost exclusively of yellow-barked acacias had served as a long-term study site for the Green Woodhoopoe. In the second half of the 1990's, the woodland was cleared for the growing of macadamia nuts and wine grapes. This loss of habitat for the woodhoopoes and other species occupying the open woodland was not due directly to the needs of local peoples, but, rather, was the result of a commercial enterprise designed to provide "luxury" items for sale primarily in Europe. The land is owned by a wealthy Kenyan, the operation is financed by Japanese interests, and the wine-growing expertise is provided by on-site German vintners. The destruction of this habitat was thus truly an international undertaking, with local Kenyan workers realizing very little of the economic benefits. This kind of situation has occurred repeatedly in Kenya, and probably in other African countries, too, as with the clearing of native habitats to grow carnations and other flowers for air shipment to Europe during the northern winter. It is worth emphasizing that this pernicious problem, whether it be concerned with the production of nuts, wine or flowers, is not the direct result of the extreme human population growth in Kenya and elsewhere in sub-Saharan Africa; rather, it is based on the economic buying power of distant developed nations.

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PLATE 33



## Subfamily PHOENICULINAE

### Genus *PHOENICULUS* Jarocki, 1821

#### 1. Forest Woodhoopoe

##### *Phoeniculus castaneiceps*

**French:** Irrisor à tête brune **German:** Waldhüp **Spanish:** Abubilla-arbórea Cabeciparda  
**Other common names:** Chestnut-headed Woodhoopoe

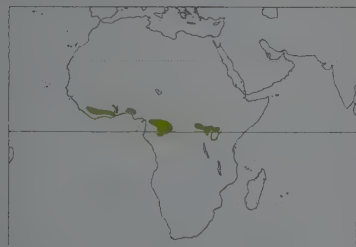
**Taxonomy.** *Irrisor castaneiceps* Sharpe, 1871, Fanti, Ghana.

Taxonomy uncertain. Although included in *Phoeniculus*, this species shares several characteristics with *Rhinopomastus* and is occasionally placed in that genus; some aspects of plumage indicate affinities with *Phoeniculus*, perhaps especially *P. bollei*, whereas size, bare-part colours and vocalizations are closer to those of *Rhinopomastus*; further DNA studies needed to clarify true generic, and hence also subfamilial, affiliation. Birds from E Zaire, Uganda and W Kenya, described as race *adolphifriederici*, now considered indistinguishable from *brunneiceps*. Two subspecies currently recognized.

##### **Subspecies and Distribution.**

*P. c. castaneiceps* (Sharpe, 1871) - Liberia E to Nigeria.

*P. c. brunneiceps* (Sharpe, 1903) - Cameroon, Gabon and Congo through Zaire to Uganda; formerly extreme W Kenya.



**Descriptive notes.** 26-28 cm; 22-25.5 g. Small, slender, dark woodhoopoe with long tail. Nominative male with rich chestnut head; back iridescent blue-green or green-blue; tail violet; wings dark blue with greenish gloss; no white in wings or tail; lower breast and belly dull greenish-black; bill relatively short and straight, grey, shading to black at base, with yellow along cutting edge; eye dark brown; tarsi and feet black. Female smaller than male, and with less iridescence. Immature like female. Male of race *brunneiceps* polymorphic, with head light chestnut-brown, pale brown, white, or black with green gloss.

**Habitat.** Canopy of primary forest, secondary growth and forest edge, also edges of clearings. Recorded from near sea-level to 1500 m. May have some subtle preferences within the forest habitat: no specimens obtained by collectors at low-elevation forest in W Uganda, but series of birds taken at a site not far away at somewhat higher elevation.

**Food and Feeding.** Mostly arthropods, including adult beetles, cockroaches, spiders, ants and termites, including alates, also caterpillars, various larvae and pupae; also small fruits, berries, seeds. Apparently almost always forages high in trees, above 25 m, occasionally descending lower, to c. 15 m. Agile, often creeping or hopping along branches, twigs, epiphytes and creepers; clings head downwards and hangs beneath branches; probes crevices for prey, also probes fruits and flowers for insects; opens rolled-up leaves. Termites captured in flight. Forages alone or in pairs, often as small groups of up to 5 or 6. Joins mixed-species foraging flocks.

**Breeding.** Nest with young in Liberia in early Apr; birds in Uganda and Zaire with enlarged gonads in Nov-Dec. Only known nest was sited in tree hole 35 m above ground; young fed by both parents at 10-minute intervals. Breeding biology otherwise entirely unknown.

**Movements.** Resident; probably sedentary within forest.

**Status and Conservation.** Not globally threatened. Numbers of this inconspicuous and little-known species entirely unknown; apparently locally common in uncut forest; not uncommon in Liberia. Threats to its continued existence consist of destruction of forest habitat: e.g., probably no longer occurs in W Kenya, as a result of deforestation in that region; several tracts of forest in W Uganda have also been largely or completely destroyed, almost certainly leading to this species' disappearance from those areas. Present in several national parks, e.g. Tai Forest (Ivory Coast) and Korup (Cameroon).

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#### 2. White-headed Woodhoopoe

##### *Phoeniculus bollei*

**French:** Irrisor à tête blanche **German:** Weißmaskenhüp **Spanish:** Abubilla-arbórea Cabeciblanca  
**Other common names:** Buff-headed Woodhoopoe

**Taxonomy.** *Irrisor Bollei* Hartlaub, 1858, Ashanti, Ghana.

Relationships uncertain; possibly closest to *P. castaneiceps*. Three subspecies recognized.

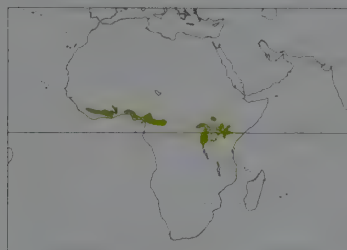
##### **Subspecies and Distribution.**

*P. b. bollei* (Hartlaub, 1858) - Liberia to S Cameroon and Central African Republic.

*P. b. okuensis* Serle, 1949 - W Cameroon (Mt Kilum).

*P. b. jacksoni* (Sharpe, 1890) - S Sudan, and E Zaire to Kenya.

**Descriptive notes.** 30-35.5 cm; 45-68 g. Nominative male with forecrown, face, chin and throat buffish-white; remainder of plumage dark and iridescent, much of body plumage and rectrices and remiges tinged blue or blue-violet, wing-coverts coppery violet; no white in either wings or tail; bill decurved, bright red; eye dark brown; legs and feet red. Female with smaller body size and, espe-



cially, much shorter bill. Juvenile with dark bill; some immatures with dark head; variable amount of white on head probably often related to age. Races differ in extent of white, in whiteness of head and in shades of body colour: *jacksoni* with forehead, forecrown, face, chin and throat white, tertials less violet than nominate; *okuensis* with white restricted to forehead, chin, upper throat, and sometimes anterior part of ear-coverts.

**Habitat.** Inhabits lowland and montane primary forest, secondary growth, sometimes more open deciduous woodland and riverine forest in wooded savanna; only member of fam-

ily to occupy highland forest. From sea-level in W Africa to up to 3200 m in montane forest of Kenya, Uganda and Zaire.

**Food and Feeding.** Primarily arthropods, including adult and larval beetles, earwigs, grasshoppers, ants, termites, spiders (including egg cocoons), caterpillars; also small berries and seeds. Forages on trunks, branches and twigs high in canopy. Uses wings and tail for support when climbing; searches undersides of branches, probes crevices in bark and lichens, opening and breaking off pieces by means of gaping action; searches epiphytes; also hammers at dead wood with bill closed. Gregarious, in groups of 2-10, occasionally more.

**Breeding.** Evidence of breeding almost throughout year over entire range, in both wet and dry seasons; apparently lays in Ghana in May-Jun; breeds in Nigeria in Jan, Mar, Oct and Nov, in Uganda in Mar and May, and in Kenya in most months. Co-operative breeder, in small groups. Nest located in natural cavity or old woodpecker hole, in living or dead tree, up to 40 m above ground; no nest material. 2 eggs recorded, but clutch size probably more variable.

**Movements.** Resident; individual birds probably highly sedentary, no movements recorded.

**Status and Conservation.** Not globally threatened. No population estimates available, so numbers of individuals entirely unknown; reasonably common resident of highland forest in Kenya; uncommon to not uncommon in Liberia. Present in several national parks, e.g. Tai Forest (Ivory Coast), Kibale Forest and Bwindi Forest (Uganda), Aberdare (Kenya) and Kibira (Burundi); also in other protected areas, e.g. Kakamega Nature Reserve (Kenya) and Nyungwe Forest Reserve (Rwanda). As with other forest-dwelling species of tropical Africa, the greatest threat is destruction of forest in which this species occurs. Deforestation may be particularly critical for subspecies *okuensis*, which occurs in an extremely restricted area around Mt Kilum (Oku) in Cameroon, where forest clearance has been going on for some time.

**Bibliography.** Bannerman (1953), Betts (1966), Britton (1980), Brown & Britton (1980), Chapin (1939), Colston & Curry-Lindahl (1986), Davidson (1975), Demey (1995), Dowsett (1990), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgood, Heigham *et al.* (1994), Friedmann (1930a), Friedmann & Williams (1971), Fry *et al.* (1988), Garshore *et al.* (1995), Gatter (1988, 1997), Gee & Heigham (1977), Grimes (1987), Halleux (1994), Holman (1947), Irvine, G. & Irvine (1991), Jackson & Selater (1938), Lewis & Pomeroy (1989), Lippens & Wille (1976), Löhrl (1972), Louette (1981a, 1981b), Mackworth-Praed & Grant (1957, 1970), Nikolaus (1987), Oberholser (1945), Robinson (1972), Serle (1949, 1950a, 1950b), Short *et al.* (1990), Snow (1978), Thiollay (1985a), Zimmerman *et al.* (1996).

#### 3. Green Woodhoopoe

##### *Phoeniculus purpureus*

**French:** Irrisor moqueur **German:** Baumhüp **Spanish:** Abubilla-arbórea Verde  
**Other common names:** Red-billed Woodhoopoe

**Taxonomy.** *Promerops purpureus* J. F. Miller, 1784, India and Africa = Cape Province, South Africa.

Generally considered to form a superspecies with *P. somaliensis* and *P. damarensis*. All three sometimes treated as conspecific, which may be a more realistic treatment; more study needed. All races apparently intergrade in areas where boundaries meet; birds from W Uganda (*ruwenzorae*) and Natal (*zuluensis*) considered inseparable from *marwitzi*; *erythrorhynchos* is a synonym of nominate *purpureus*. Six subspecies recognized.

##### **Subspecies and Distribution.**

*P. p. guineensis* (Reichenow, 1902) - N Senegal and Mali to N Ghana, Nigeria, Chad and Central African Republic.

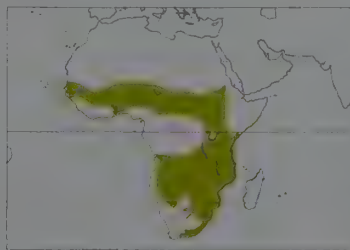
*P. p. senegalensis* (Vieillot, 1822) - S Senegal and Gambia E to S Ghana.

*P. p. niloticus* (Neumann, 1903) - Sudan, W Ethiopia and NE Zaire.

*P. p. marwitzi* (Reichenow, 1906) - E Uganda and Kenya S to C & E Natal; also extreme S Somalia (2 records).

*P. p. angolensis* (Reichenow, 1902) - Angola and Namibia E to W Zambia and W Zimbabwe.

*P. p. purpureus* (J. F. Miller, 1784) - Cape Province E to Transkei.



**Descriptive notes.** 32.5-37 cm; 54-99 g. A large, frequently noisy woodhoopoe. Nominative adult green-glossed; head and throat bluer, nape violet, upper mantle blue; tail graduated and with white subterminal spots; wings with white bar across middle of primaries, primary coverts white only at tips; bill red; tarsi and toes red. Female like male but smaller, with shorter bill. Juvenile without iridescence, and with short dark bill and dark feet; most juvenile males and some females have brown or buff throat; tail spots reduced. Races differ in shade of iridescence and in extent of white on rectrices and remiges, while

body size decreases from W to E and from N to S, all races being larger than nominate: *marwitzi* is iridescent, with crown, chin, nape and face blue, neck blue-green, mantle, scapulars, throat and breast green, and has white subterminal spot on both webs of outer 2-3 rectrices and white bar on middle of outer webs of primaries; *angolensis* like previous, but blue more extensive on nape and throat, tail spots larger than in nominate; *niloticus* duller and darker than *marwitzi*, crown, nape and mantle deeper violet-blue; *guineensis* like previous, but crown and face more blue-green,

wing longer, tail shorter; *senegalensis* like previous, but crown, nape and mantle duller, mantle more violet, bill may be partly or completely black.

**Habitat.** Over its huge range, occurs in wide variety of habitats, including savanna, open woodland, palm groves, riverine forest in arid thornbush country, and wooded gardens, from near sea-level to well over 2000 m. Absent from arid zones and forest. A key requirement is trees large enough to hold cavities for roosting and nesting.

**Food and Feeding.** Diet consists mostly of arthropods, including adult and larval moths, insect and spider egg masses, beetle larvae, pupae and adults, winged and unwinged termites; occasionally centipedes, millipedes, spiders, solifugids and vertebrates (small lizards), and small fruits. In Kenya, over 90% of food brought to nestlings was caterpillars. Forages on trunks, branches and twigs; some sexual segregation of foraging sites, with males tending to search lower down on trunks and large branches, females tending to forage higher and using the smaller branches, limbs and twigs; sometimes on ground, or on termite mound. Forages in acrobatic fashion, often hanging beneath or on sides of branches; peers and probes into holes and crevices in bark; can hammer bark loose, also pry bark loose with gaping action. Prey often treated by pounding and rubbing against bark before ingestion. Usually in groups of 4-8, occasionally much larger groups of up to 16 birds.

**Breeding.** Over large range, breeding activity recorded in every month, in tropical regions usually associated with rain: in Senegambia in Apr and Jun, in Ghana in all months, in Nigeria in Jan, Feb and Aug, in Chad in Jul-Sept, in Sudan in Oct-Nov; in Kenya, typically in Jun, following termination of "long rains"; second and even third nestings by same birds may occur during year if food conditions, which greatly affected by amount and timing of rainfall, are suitable; in South Africa, breeding typically occurs only in Sept-Nov, and no more than 1 brood per year. Co-operative breeder, in small to medium-sized groups with helpers. Nest in tree cavity, either natural or old woodpecker or barbet hole; rarely in unexpected site, e.g. in hole in support post in barn, or directly on ground underneath farm machinery in shed, or in housing of air conditioner. Most clutches in Kenya of 3-4 eggs, rarely 2 or 5; only breeding female incubates; incubation period 17-18 days. Parasitized by Greater Honeyguide (*Indicator indicator*).

**Movements.** Mostly resident; possible seasonal movement in W Africa. Highly philopatric in Kenya and South Africa; most individuals of both sexes either breed in territory in which they hatched or move only 1-4 territories to acquire breeding status.

**Status and Conservation.** Not globally threatened. Extremely widespread geographically, and often common; in Senegambia, common to locally abundant; in Sierra Leone patchily distributed, locally not uncommon, but absent from several areas; in Kenya, locally common in wooded habitat, but scarce away from water in arid areas, probably because large trees occur along watercourses. Destruction of prime habitat, as at L Naivasha in Kenya, can devastate local populations. Present in numerous national parks, e.g. Mole (Ghana), Waza and Kalamaloué (Cameroon), Nakuru and Tsavo (Kenya), Serengeti (Tanzania), Liwonde and Lengwe (Malawi) and Kruger (South Africa).

**Bibliography.** Anon. (1998c), Ash & Miskell (1998), Bannerman (1953), Barlow *et al.* (1997), Benson & Benson (1948), Benson *et al.* (1971), Boix-Hinzen & Lovegrove (1998), Britton (1980), Brown & Britton (1980), Bruning & Bell (1976), Cawkill & Moreau (1963), Chapin (1939), Cheke & Walsh (1996), Clancey (1964a), Davidson (1975), Dean (2000), Douthwaite (1995), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Duckworth *et al.* (1992), Elgood, Fry & Dowsett (1973), Elgood, Heigham *et al.* (1994), Field (1999), Friedmann (1930a), Fry *et al.* (1988), Ginn *et al.* (1989), Giraudoux *et al.* (1988), Gore (1990), Grimes (1975, 1976, 1987), Harrison *et al.* (1997), Irwin (1981), Jensen & Kirkeby (1980), Joubert & Joubert (1997), Jubb (1966, 1968a), Lamarche (1980), Lewis & Pomeroy (1989), Ligon (1981, 1984, 1988), Ligon & Ligon (1978a, 1978b, 1982, 1983, 1988, 1989, 1990a, 1990b), Ligon, Carey & Ligon (1988), Ligon, Carey, Ligon & Farley (1989), Lippens & Wille (1976), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Medland & Medland (1989, 1992), Morel & Morel (1990), Neuert *et al.* (1995), Newby (1980), Newman (1981), Newton-Howes (1968), Oberholser (1945), Pakenham (1979), Penry (1994), Pinto (1983), du Plessis (1988, 1989a, 1989b, 1991, 1992, 1993, 1994b), du Plessis & Williams (1994), Robertson (1995a), Rowan (1970), Rudloff (1993), Short *et al.* (1990), Snow (1978), Steyn (1996b), de Swardt (1994), Thiollay (1985a), Trendler (1997), Ward *et al.* (1989), Williams *et al.* (1991), Zimmerman *et al.* (1996).

## 4. Black-billed Woodhoopoe

### *Phoeniculus somaliensis*

**French:** Irrisor à bec noir      **Spanish:** Abubilla-arborea Piquinegra  
**German:** Schwarzschnabel-Baumhopf

**Taxonomy.** *Irrisor somaliensis* Ogilvie-Grant, 1901, Fer Libah, Ogaden, Ethiopia.

Generally considered to form a superspecies with *P. purpureus* and *P. damarensis*. All three sometimes treated as conspecific, which may be a more realistic treatment; more study needed. Race *abyssinicus* has been thought to be a hybrid of race *neglectus* and *P. purpureus niloticus*, but the two species are said to occur sympatrically without apparently interbreeding in parts of S Ethiopia and N Kenya. Three subspecies recognized.

#### **Subspecies and Distribution.**

*P. s. abyssinicus* (Neumann, 1903) - N Ethiopia and Eritrea.

*P. s. neglectus* (Neumann, 1905) - C Ethiopia.

*P. s. somaliensis* (Ogilvie-Grant, 1901) - SE Ethiopia, W Somalia and NE Kenya.

**Descriptive notes.** 33-38 cm. Blackish plumage with much iridescence, mainly violet and blue-violet. Nominale race with feathers of crown, face and nape green, fringed violet; throat feathers greenish-copper, fringed violet; white bar on primaries, white subterminal patches on rectrices; iris dark brown; bill black, sometimes bright red at base; tarsi and toes bright red. Differs from *P. purpureus* in more slender and more strongly decurved bill. Sexes alike. Immature dull black, with variable amount of buff on feathers of chin and throat; bill and legs dark. Races differ slightly in plumage coloration: *neglectus* with crown, nape and mantle greener, back brighter violet; *abyssinicus* with crown and nape deep greenish-violet, mantle and breast greener, and bill red at base, especially on lower mandible.



**Habitat.** Open dry thornbush and riparian woodland, woodland edge, and scattered trees along dry wadis. From near sea-level to 1500-2000 m.

**Food and Feeding.** Arthropods, including beetles and millipedes. Forages by moving up and down trunk and branches, sometimes head downwards, probing crevices. Often in noisy groups of 10-12 birds.

**Breeding.** In N Somalia Feb-Sept, with 6 of the 8 records in mid-May to mid-Jun. Mating system not known, but group-living behaviour like that of *P. purpureus* suggests co-operative breeding. Nest in cavity of living or dead

tree, either natural cavity or woodpecker hole; no nesting material beyond rotted wood in cavity. 3-5 eggs, average 4.0.

**Movements.** Not known; probably sedentary, with large territory.

**Status and Conservation.** Not globally threatened. No population estimates available, but apparently not rare; in Somalia, common in N & NW and less common in S; fairly common resident of open bush and riparian woodland in much of NE Kenya. Only current threat related to human activities is cutting of trees large enough to hold cavities. Present in Awash National Park (Ethiopia).

**Bibliography.** Archer & Godman (1937-1961), Ash & Miskell (1998), Britton (1980), Cheesman & Sclater (1935), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Duckworth *et al.* (1992), Friedmann (1930a), Fry *et al.* (1988), Jackson & Sclater (1938), Lewis & Pomeroy (1989), Mackworth-Præd & Grant (1957), Moltoni (1940), Nikolaus (1987), Oberholser (1945), Robertson (1995a), Short *et al.* (1990), Smith (1957), Snow (1978), Urban & Brown (1971), Zimmerman *et al.* (1996).

## 5. Violet Woodhoopoe

### *Phoeniculus damarensis*

**French:** Irrisor damara      **German:** Steppenbaumhopf      **Spanish:** Abubilla-arborea Violeta  
**Other common names:** Grant's Woodhoopoe (*granti*); Southern Violet Woodhoopoe (*damarensis*)

**Taxonomy.** *Irrisor damarensis* Ogilvie-Grant, 1901, Damaraland.

Generally considered to form a superspecies with *P. purpureus* and *P. somaliensis*. All three sometimes treated as conspecific, which may be a more realistic treatment; more study needed. Race *granti*, geographically isolated by huge distance from nominate race, sometimes given full specific rank, but this is currently considered inappropriate, particularly in light of confusion regarding taxonomic treatment of present species; further research required. Two subspecies recognized.

#### **Subspecies and Distribution.**

*P. d. granti* (Neumann, 1903) - S Ethiopia and Kenya.

*P. d. damarensis* (Ogilvie-Grant, 1901) - W Angola and NW Namibia.



**Descriptive notes.** 34.5-38 cm; 72-96 g. A very dark, large woodhoopoe. Nominale race with dark coppery purple iridescence on crown, face, nape, mantle, back and rump; chin and throat blue-green; breast and upper belly coppery purple; white bar on primaries, subterminal white spots on outer tail feathers; bill decurved, bright red, sometimes black at base; eye dark brown; tarsi and toes bright red. Differs from *P. purpureus* and *P. somaliensis* in having iridescence mostly dark purple-violet, rather than green of former or violet and blue of latter. Sexes similar. Immature duller than adult, with short, black bill. Race *granti*

smaller, with iridescence brighter and less coppery, the crown, nape, mantle, scapulars and wings more violet, and throat and breast bluer, with feathers fringed coppery violet; variable amounts of black at base of bill, although this feature might be merely age-related.

**Habitat.** Dry *Acacia* scrub and thornbush, often around watercourses and palm trees, from sea-level to 1500 m.

**Food and Feeding.** Mostly insects, including beetles, grasshoppers, caterpillars, pupae, beetle larvae; also takes eggs from nests of small birds such as weavers (Ploceidae). Gregarious, in groups of 2-12 birds.

**Breeding.** Nominale race breeds Jul-Sept, Jan and Feb. Mating system not known, but group-living behaviour like that of *P. purpureus* suggests co-operative breeding. Nest in cavity of living or dead tree. Only 1 known clutch, of 3 eggs.

**Movements.** Movements unknown, but probably sedentary, with large territory.

**Status and Conservation.** Not globally threatened. No population estimates available; in Kenya, local and uncommon resident in bush and riverine woodland in E, mainly below 1000 m. Only present threat posed by human activities is destruction of trees large enough to hold cavities suitable for nesting and roosting. Present in Etosha National Park (Namibia).

**Bibliography.** Bennun & Njoroge (1996, 1999), Boix-Hinzen (1998b), Britton (1980), Brown (1963), Brown & Britton (1980), Clancey (1964), Dean (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Duckworth *et al.* (1992), Friedmann (1930a), Fry *et al.* (1988), Ginn *et al.* (1989), Harrison *et al.* (1997), Jackson & Sclater (1938), Kaestner & Kaestner (1978), Lewis & Pomeroy (1989), Mackworth-Præd & Grant (1957, 1962), Maclean (1993), Oberholser (1945), Pinto (1983), Short *et al.* (1990), Snow (1978), Steyn (1996b), Urban & Brown (1971), Zimmerman *et al.* (1996).







PLATE 34

inches 3  
cm 8



## Subfamily RHINOPOMASTINAE

### Genus *RHINOPOMASTUS* Jardine, 1828

#### 6. Black Woodhoopoe

##### *Rhinopomastus aterrimus*

**French:** Irrisor noir **German:** Mohrenschelhopf **Spanish:** Abubilla-arborea Negra  
**Other common names:** Black Scimitarbill, Lesser/Scimitar-billed Woodhoopoe

**Taxonomy.** *Promerops aterrimus* Stephens, 1826, Senegal.

Taxonomy rather complicated, and much debated. Genus often merged into *Phoeniculus*. In past, under arrangement with division of family into three genera, present species was commonly placed in monospecific *Scoptelus*, based on rather straight bill. Even under arrangement dividing family into two genera, present species was often placed in *Phoeniculus*, but DNA studies in particular indicate closer phylogenetic affinities with *Rhinopomastus*. Forms a superspecies with *R. cyanomelas*; these two sometimes considered conspecific, intergrading in S Angola and SE Zaire, with hybridization also documented, but elsewhere (e.g. W Zambia) they appear ecologically separated; differences in morphology and vocalizations also suggest they are probably better treated as separate species. Birds from Angola and W Zambia, described as race *anomalous*, now considered inseparable from *anchietae*; those from Sudan described as *cavei* apparently inseparable from *notatus*. Four subspecies recognized.

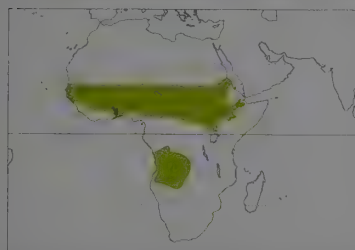
##### **Subspecies and Distribution.**

*R. a. aterrimus* (Stephens, 1826) - Senegambia E to W Sudan.

*R. a. emini* (Neumann, 1905) - C Sudan to NE Zaire and Uganda.

*R. a. notatus* (Salvin, 1892) - E Sudan and Ethiopia; recently recorded also in NW Somalia.

*R. a. anchietae* (Bocage, 1892) - S Zaire and Angola to W Zambia.



less decurved black bill. Races differ in shades of blue and violet and in amount of white on wings and tail: *emini* slightly larger than nominate, wings and tail sometimes bluer, white of primaries often restricted to inner webs, fewer primary coverts white (sometimes invisible on closed wing), tail of some birds with white subterminal spot or bar on outer feathers only; *notatus* similar in size to previous, but bluer, no white on primary coverts or white on innermost only, tail with variable broader white spot or bar on outermost feathers; *anchietae* like *emini*, but wing and tail longer and bill smaller, nape and mantle brighter violet-blue, wings and tail brighter blue, white bar on primaries broader, no white on primary coverts, tail with broad white subterminal band on outer 2 rectrices, sometimes also on third rectrix.

**Habitat.** Wooded savanna and dry bush country to limit of trees; avoids forest. From sea-level to over 2000 m.

**Food and Feeding.** Mostly insects, including ants and their larvae, adult beetles, mantids, caterpillars, pupae; also spiders, small berries. Forages in bushes and trees, mostly in canopy on twigs and small branches, also on trunks, and occasionally on ground. In Ghana, foraged 76% of time on branches less than 5 cm thick, 73-5% of time on dead wood. Agile, hangs upside-down and drops or dives vertically; probes crevices, also searches flowers for insects. Solitary, or in pairs or small family groups. Often in mixed-species foraging parties.

**Breeding.** Recorded in Apr. Jun-Jul and Sept-Jan; in Gambia, nest with young in mid-Oct, fledged young in late May and Oct. Monogamous; solitary nester; only 2 adults at nest, no helpers. Nest in tree cavity. Clutch size and incubation period uncertain; male delivers food to female, which then feeds young; later, both sexes forage together; female takes food from male at nest entrance and delivers it to nestlings.

**Movements.** In Nigeria, withdraws S into guinea savanna in dry season; population fluctuations suggest similar migratory movements elsewhere in W Africa.

**Status and Conservation.** Not globally threatened. No population estimates available; species is very widespread and in some areas locally common; frequent to very locally common in S half of W Gambia; widespread but nowhere common in Senegal. The only current known threat posed by human activities is destruction of trees that species uses for foraging, nesting and roosting in. Present in numerous national parks, e.g. Niokola Koba (Senegal), Comoe (Ivory Coast), Mole (Ghana), W (Niger), Waza (Cameroon), Bamingui-Bangoran (Central African Republic) and Dinder (Sudan).

**Bibliography.** Ash & Miskell (1998), Bannerman (1953), Barlow *et al.* (1997), Bates (1927), Beel & Leonard (1996), Benson & Irwin (1965, 1968), Blasdale (1984), Britton (1980), Cawell & Moreau (1963), Chapin (1939), Cheke & Walsh (1996), Davidson (1975), Dean (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dowsett-Lemaire & Dowsett (1998), Elgood, Fry & Dowsett (1973), Elgood, Heigham *et al.* (1994), Field (1999), Friedmann (1930a), Fry *et al.* (1988), Giraudeau *et al.* (1988), Gore (1990), Grimes (1987), Holman (1947), Jackson & Selater (1938), Jensen & Kirkeby (1980), Lamarche (1980), Lippens & Wille (1976), Macdonald (1946), Mackworth-Praed & Grant (1957, 1962, 1970), Morel & Morel (1990), Nikolaus (1987), Pinto (1983), Serle (1957), Short *et al.* (1990), Snow (1978), Thiollay (1985a), Traylor (1960a, 1964, 1965), Urban & Brown (1971).

#### 7. Common Scimitarbill

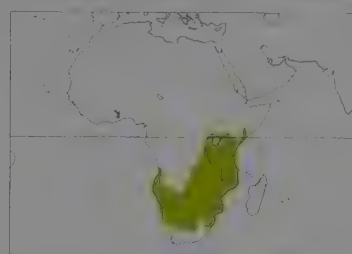
##### *Rhinopomastus cyanomelas*

**French:** Irrisor namaquois **German:** Scitelhopf **Spanish:** Abubilla-arborea Cimitarra  
**Other common names:** (Greater) Scimitarbill

**Taxonomy.** *Falcinellus cyanomelas* Vieillot, 1819, Orange River, north-western Cape Province. Genus often merged into *Phoeniculus*. Present species forms a superspecies with *R. aterrimus*; these two are sometimes considered conspecific, intergrading in S Angola and SE Zaire, with hybridization also documented, but elsewhere (e.g. W Zambia) they appear ecologically separated; morphological and vocal differences also suggest they are probably better treated as separate species. Birds from Zimbabwe, S Mozambique and E South Africa (Transvaal, Zululand), described as *intermedius*, now regarded as inseparable from *schalowi*. Two subspecies currently recognized.

##### **Subspecies and Distribution.**

*R. c. schalowi* Neumann, 1900 - W Uganda, W & C Kenya and S Somalia S to Zambia and W Natal.  
*R. c. cyanomelas* (Vieillot, 1819) - SW Angola and Namibia E to Transvaal.



**Descriptive notes.** 26-30 cm; 24-38 g. Nominant male dark, iridescent, with crown and face deep blue, nape, mantle and rump violet; white bar across primaries, some primary coverts white; white subterminal spots may be present or absent on outer tail feathers; underparts dull black with blue tinge; bill long, slender, strongly decurved, black; eye dark brown; tarsi and toes black. Female like male but smaller, perhaps duller and browner below. Immature duller than adult, with short black bill. Race *schalowi* longer-tailed but shorter-billed, broad white bar on inner web of primaries, spot present on outer web of pri-

maries 2-9, outer half of primary coverts white, tail with variable broad white subterminal bar on outer three feathers.

**Habitat.** Dry thornbush country, palms, wooded savanna, occasionally thicker woodland, but avoids true forest. From sea-level to over 2000 m.

**Food and Feeding.** Diet consists mostly of insects, including ants and their larvae from ant-galls, as well as flies, caterpillars, pupae; also spiders, small fruits, berries, tree seeds. Forages on branches, twigs, foliage and flowers for insects. Frequently hangs upside-down, and climbs down trunk head downwards; probes small holes in galls of ant-gall acacia (*Acacia drepanolobium*); sometimes forages on ground. Solitary, or in pairs or small family groups. Often joins mixed-species foraging flocks.

**Breeding.** Recorded Aug-Feb; in Zimbabwe most records Sept-Oct; Aug and Oct in Zambia, Sept-Oct in Namibia; in South Africa Jan and Sept-Dec, with most records in Oct-Nov; in Kenya, nesting recorded in Jun. Monogamous; solitary nester; no helpers at nest recorded. Nest in tree cavity, either natural cavity or old woodpecker hole; some material (dead leaves, lichens) brought to nest; in Kenya (L. Naivasha), pair nested very close to active *Phoeniculus purpureus* nest; same site may be used in successive years. 2-4 eggs, average 3.24 in Zimbabwe, Zambia and Malawi, 3.0 in South Africa; chick covered with long quills at 10 days, quills shed rapidly, leaving complete new juvenile plumage; female remains at nest with small young; male delivers food to female, which then feeds young; later, both parents forage, usually together, often returning to nest together, where each feeds young.

**Movements.** Movements of individuals unknown, but species is probably less sedentary than *Phoeniculus* species.

**Status and Conservation.** Not globally threatened. No population estimates available; widespread and sometimes locally common; fairly common resident in open woodland, savanna and bush across much of N Tanzania and S Kenya; uncommon in S Somalia. Only presently known threat posed by human activities is destruction of trees used for foraging, nesting and roosting. Present in numerous national parks, e.g. Akagera (Rwanda), South Luangwa (Zambia), Hwange and Mana Pools (Zimbabwe), Etosha (Namibia) and Kruger (South Africa).

**Bibliography.** Ash & Miskell (1998), Benson & Irwin (1965, 1968), Benson *et al.* (1971), Britton (1980), Brown & Britton (1980), Chapin (1939), Clancey (1961, 1964a), Cole (1992), Dean (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Friedmann (1930a), Fry *et al.* (1988), Ginn *et al.* (1989), Harrison *et al.* (1997), Hines (1995), Hoesch (1933a), Irvine, D. & Irvine (1991), Irwin (1998), Jackson & Selater (1938), Jones & Ayre (1987), Lewis & Pomeroy (1989), Lippens & Wille (1976), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Penry (1983), Short *et al.* (1990), Snow (1978), Sleyen (1996b), Traylor (1960a, 1965), Turner, Pearson & Zimmerman (1991), White (1965), Winterbottom (1949), Zimmerman *et al.* (1996).

#### 8. Abyssinian Scimitarbill

##### *Rhinopomastus minor*

**French:** Irrisor à cimeterre **German:** Goldschnabelhopf **Spanish:** Abubilla-arborea Menor

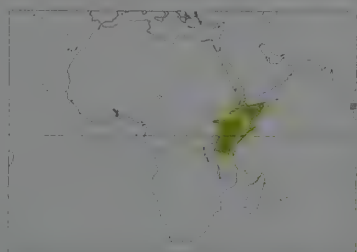
**Taxonomy.** *Promerops minor* Rüppell, 1845, Shoa, central Ethiopia.

Genus often merged into *Phoeniculus*. Birds from S Somalia and adjacent N Kenya, described as race *somalicus*, are now considered inseparable from nominate *minor*; birds from S Kenya to Tanzania, formerly recognized as race *extimus*, now treated as indistinguishable from *cabanisi*. Two subspecies currently recognized.

##### **Subspecies and Distribution.**

*R. m. minor* (Rüppell, 1845) - Ethiopia (except S), Somalia and NE Kenya.

*R. m. cabanisi* (de Filippi, 1853) - S Sudan, S Ethiopia and N & NW Kenya S to N Tanzania.



**Descriptive notes.** 21-24 cm; 28-30 g (3 birds). Smallest member of family; noticeably slender. Plumage mainly dark, feathers on upperparts with some violet-blue iridescence. Nominant race with entire upperparts violet-blue, broad white bar on primaries; no white spots on tail; bill decurved, bright orange; eye dark brown; tarsi and toes black. Female like male but slightly smaller and duller; much browner below. Immature duller than adult, with brownish underparts, shorter dusky bill darker at tip. Race *cabanisi* larger than nominate, and underside, in particular, may be duller, also lacks white bar on primaries.

**Habitat.** Inhabits light woodland, dry *Acacia* bush and thorn-scrub, especially along dry water-courses; also scattered trees in open grassland in Somalia. From sea-level to 2000 m; commonest at 1000-1300 m.

**Food and Feeding.** Mostly insects, including both adults and larvae: beetles, Lepidoptera, ants, flies, wasps. Occasionally seeds and berries. Forages on trunks and branches of trees. Probes crevices and under bark for insects; also searches flowers and fruits; descends trunks and hangs beneath branches. Solitary, or in pairs or small family groups.

**Breeding.** Recorded Dec-Jul, most breeding in dry season: in Somalia in Apr-Jun/Jul, in Ethiopia in Feb-May, in Uganda in Jan and Apr, in Kenya in Jan-Jul. Monogamous; solitary nester; only 2 adults at nest, no helpers. Nest in tree cavity; no nest material. 2-3 eggs, average 2.8. Parasitized by Greater Honeyguide (*Indicator indicator*).

**Movements.** Neither seasonal movements nor movements of individuals recorded.

**Status and Conservation.** Not globally threatened. No population estimates available; species is locally common in some areas; generally rare in S Sudan; widespread and fairly common in

Somalia; in Kenya, generally rather uncommon but sometimes considered to be common locally in bush and open woodland of drier areas; widespread in inland N Tanzania. The only known current threat posed by human activities is the destruction of trees used by the species for foraging, nesting and roosting in. Present in several protected areas, e.g. Serengeti National Park (Tanzania) and Samburu Reserve (Kenya).

**Bibliography.** Archer & Godman (1937-1961), Ash & Miskell (1998), Britton (1980), Brown & Britton (1980), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Friedmann (1930a), Fry *et al.* (1988), Jackson & Selater (1938), Lewis & Pomeroy (1989), Mackworth-Praed & Grant (1957), Madge & Cunningham-van Someren (1975), Nikolaus (1987), Robertson (1997), Schmidt (1982), Short *et al.* (1990), Snow (1978), Turner, Pearson & Zimmerman (1991), Urban & Brown (1971), White (1965), Zimmerman *et al.* (1996).





Class AVES  
Order CORACIIFORMES  
Suborder BUCEROTES  
**Family BUCEROTIDAE (HORNIBILLS)**



- Medium-sized to very large birds with long, curved bill surmounted by hollow casque; broad, rounded wings and long tail.
- 30-120 cm.



- Afrotropical and Oriental; marginal in Australasian.
- Mainly forest; also woodland and savanna.
- 14 genera, 54 species, 78 taxa.
- 9 species threatened; at least one subspecies probably extinct since 1600.

### Systematics

The Bucerotidae are one of the most recognizable groups of all birds. The long, decurved bill is their most obvious feature, this being surmounted by a casque that is unique among avian families. In many hornbill species the casque is developed as a large, imposing structure. Through both their active behaviour and their loud calls, the hornbills are among the most conspicuous of birds wherever they occur across sub-Saharan Africa and South-east Asia. The only birds with which they might conceivably be confused are the toucans (Ramphastidae) of South America, which are small to medium-sized birds that also have a large and brightly coloured bill, but which are most closely related to the barbets (Capitonidae) and the woodpeckers (Picidae).

Traditional classifications have included the hornbills within the avian order Coraciiformes, mainly on the basis of a partial fusion of the base of the three front toes, a condition known as syndactyly. Other groups of birds with a similar foot arrangement are the hoopoes (Upupidae), the woodhoopoes and scimitarbills (Phoeniculidae), the rollers (Coraciidae), the bee-eaters (Meropidae), the kingfishers (Alcedinidae), the todies (Todiidae) and the motmots (Momotidae). The nestlings of all these families also share two features: the protrusion of the lower jaw well past the upper jaw for a few days after hatching, and the retention of feathers in the quill for a prolonged period after emergence, the latter a phenomenon that creates a "porcupine-like" or "pin-cushion-like" stage of development.

More recent studies, including detailed anatomical comparisons and such molecular techniques as DNA-DNA hybridization, have supported the idea of a broad general relationship among these diverse groups of birds. They have also altered our understanding of affinities between families within the assemblage, besides highlighting the association with other, less obviously related groups such as the cuckoo-rollers (Leptosomidae), the ground-rollers (Brachypteraciidae), the trogons (Trogonidae), the puffbirds (Bucconidae) and the jacamars (Galbulidae), even though they possess a rather different foot structure. The last two families, however, are just as frequently placed together with the barbets and the toucans in the Piciformes, which also includes the honeyguides (Indicatoridae) and the woodpeckers themselves.

Another theory, now gaining a wider consensus, is that the hornbills are probably sufficiently different from all other bird families to be assigned an order of their own, the Bucerotiformes, while their nearest relatives, almost certainly the hoopoes and

the woodhoopoes and scimitarbills, are also commonly recognized as meriting their own order, the Upupiformes. These two groups lack the bright colours evident in the plumage of so many other coraciiforms, and their eggs are elongated with pitted shells, in contrast to the smooth, rounded eggs of other groups. If this treatment is followed, the remaining coraciiform families are still regarded as being related, but rather more distantly, and with only some of them still included in a more restricted Coraciiformes order.

Whatever level of taxonomic classification the family is accorded, there is really never any doubt about what constitutes a hornbill. Besides the prodigious bill and the casque, which grows from a special area of vascularized tissue at the front of the skull (see Morphological Aspects), there are several other anatomical



Subdivision of the  
Bucerotidae

[Figure: Tim Worfolk]



In the Old World, to which they are confined, hornbills are amongst the most distinctive of birds.

They attract attention to themselves by their large size, conspicuous behaviour and loud calls, and are easily recognized because of their massive bills. Many species of hornbill eat fruit and live in trees, but this is by no means the only lifestyle they have adopted.

Southern Ground-hornbills, for example, are terrestrial and principally carnivorous. Indeed, the peculiarities of the two ground-hornbill species have led to their isolation within the subfamily Bucorvinae; indeed, recent evidence suggests that they are so distantly related from other hornbills that they belong in a separate family altogether.

[*Bucorvus leadbeateri*,  
Kruger National  
Park, South Africa.  
Photo: Jean-Paul Ferrero/  
Auscape]



details that are unique to the hornbills and which further define their position in a monophyletic clade. In particular, the support required for the large bill and its associated musculature has resulted in two features that exist nowhere else in the avian world. The first two neck vertebrae, the atlas and the axis, are fused and, in addition, the skull articulates on the neck with a special supraoccipital as well as a basioccipital condyle. The kidney of hornbills is also unusual, being comprised of only two lobes and lacking the third median lobe found in all other birds, although the reasons for this remain uncertain. Finally, for the few hornbill species that have been appropriately studied to date, smears of their cell nuclei reveal that the Z chromosome, one of the pair of Z and W sex chromosomes, is always the largest chromosome in the nucleus. Furthermore, several external features that are peculiar to the hornbills are more obvious, such as the well-developed flattened lashes on the upper eyelid and, under the wing, the lack of covert feathers over the forearm and the bases of the primaries and secondaries. Certain aspects of their behaviour, too, distinguish the hornbills from all other birds, the best known of which is that the female seals herself into a nest-cavity when breeding and leaves only a narrow vertical slit, through which she is fed by the male.

Within the overall assemblage of hornbills, a further division occurs between the ground-hornbills of the genus *Bucorvus* and the typical, or arboreal, hornbills. There are currently only two species of ground-hornbill, both confined to the open savanna of sub-Saharan Africa, and it is to that group that the only fossil remains known for hornbills, a femur from the leg of a species named *Bucorvus brailloni*, are assigned. This bone was unearthed from among middle Miocene deposits in Morocco, north of the present range of the genus, at an estimated date of about 15 million years ago.

Ground-hornbills are the largest living members of the family. They exhibit several traits that are deemed primitive among hornbills, despite their obvious specialization for a terrestrial existence. In particular, they have 15 neck vertebrae, whereas these are reduced to 14 in all other hornbills, and they neither seal up the entrance to their nests nor practise any form of nest sanitation. Traditionally, they have been treated as a separate sub-

family, the Bucorvinae, on the basis of their long legs, the lack of carotid arteries and the special tendon connecting the pelvis and the femur. All other hornbills have generally been placed in the subfamily Bucerotinae. On the other hand, modern molecular studies suggest that the differences between the two groups are so profound that each should be elevated to the status of a full family.

In summary, therefore, there are two extant species of ground-hornbill, both placed in the genus *Bucorvus* like their fossil ancestor. The two are best differentiated by the form of the casque and the colour of the bare facial skin. Both species have longer legs than other hornbills, and they hunt their small animal prey mainly while walking on the ground. Besides being separated from the Bucerotinae by various details of their anatomy and behaviour, they are also unusual in that they carry food to the nest as several items held together in the tip of the bill, forming a food parcel, or bolus. Like their distant relatives the hoopoes and the woodhoopoes, the ground-hornbills also call with the head bowed as they utter their deep booming notes.

Within the subfamily Bucerotinae, containing the typical hornbills, 52 species are currently recognized by virtually all modern biologists. The relationships between them, however, are not obvious, even though several natural groupings of species are fairly easy to define. Each of these groups is usually designated as a different genus, but the total number of genera that are recognized, depending on how finely the groups of species are divided, ranges from 13 in earlier classifications down to only eight in the most recent analysis. Simple as it may be to assign most species to a genus, the relationships between those genera are much more difficult to unravel. It is quite evident that certain traits are shared by species in different genera, but to date no clear pattern has emerged that shows unequivocally which genera are most closely interrelated, or what their evolutionary history may have been.

The largest genus of typical hornbills is the African *Tockus*, containing 13 species. These, too, can be characterized by the manner in which they transport food to the nest, in this case as a single item carried in the tip of the bill. These are the smallest of all hornbills, and most are inhabitants of savanna or woodland.



Apart from their method of carrying their food, which consists mainly of insects, most species also exhibit conspicuous forms of territorial display. It is of interest that not only are these displays conspicuous, but they can also be clearly separated into two distinct forms: some species raise the bill skywards and utter whistling calls, whereas others bow the head while uttering clucking calls.

Within each of these two branches of *Tockus* hornbills, respectively the "whistlers" and the "cluckers", a further dichotomy exists between species that open the wings during display and those that keep the wings closed. Each of these divisions between the species, based on behaviour, can apply to anything from two to four species, and most divisions are recognized further by classification into separate subgenera. The same behavioural divisions are also linked to other morphological and behavioural differences. The "whistlers" hop when on the ground, constrained by their shorter legs, but they fly with a buoyant floating flight on their longer wings. They usually line their nests with bark flakes, and they prefer to roost at the tip of a long thin branch. The "cluckers", on the other hand, have longer legs, with which they walk, rather than hop, on the ground, and they possess shorter wings, with which they fly in a direct flap-and-glide progression. They also line their nests mainly with foliage, and prefer to roost in a concealed position against a large tree limb.

The only exceptions to these behavioural divisions within the genus *Tockus* are two little-known species of the African rain-forest, both of which apparently lack any elaborate display. These are the dove-sized dwarf-hornbills, the smallest of all the Bucerotidae, and each one has its own special call. They are known to be attracted to other animals, be they army ants, squirrels or troops of monkeys, around which they capture the insects that are disturbed by those animals' movements. The Red-billed Dwarf-hornbill (*Tockus camurus*) is unique within the genus in that it lives in small groups, the members of which breed co-operatively.

An aberrant species, the Long-tailed Hornbill (*Tropicranus albocristatus*), is often included in the genus *Tockus*. It resembles the two dwarf species in lacking an elaborate display and, like those two, it is also attracted to other animals. The Long-tailed Hornbill, however, differs from all other Bucerotidae in that it behaves like a large flycatcher (Muscicapidae), swooping through the middle and lower canopy of the forest, steered by its



The hornbill family is currently placed in the order Coraciiformes on the basis of a range of morphological features, particularly syndactyly. However, a growing body of evidence suggests that it is sufficiently distinctive to merit an order of its own, the Bucerotiformes. This White-crowned Hornbill, and its relatives in the subfamily Bucerotinae, possess several characteristics unique amongst birds, or shared only with the Bucervinae, ranging from skeletal design to the arrangement of the feather tracts and fundamental aspects of breeding biology.

[*Berenicornis comatus*, Hala-Bala Wildlife Sanctuary, Thailand. Photo: Morten Strange]

exceptionally long, graduated tail. It is further distinguished by its copious white crest and, moreover, it has a howling call unlike that of any other hornbill. These differences are probably sufficient to justify its being accorded its own monotypic genus, *Tropicranus*.

The final two African genera, *Bycanistes* and *Ceratogymna*, between them contain seven species of forest hornbill which are quite different from the large carnivorous ground-hornbills and the small insectivorous *Tockus* hornbills of the savannas. They are intermediate between those two genera in size, and are predominantly black in plumage colour, but they display various areas of pure white on the body and on the tips of the wings and tail. A characteristic of all members of both *Bycanistes* and *Ceratogymna* is that the adult male has a much larger casque than does the adult female, and indeed, in several species, the male's casque is proportionately among the largest of any of the Bucerotidae. These forest hornbills, and especially the males, have particularly loud calls with a peculiar nasal quality. Since the large casque of these species is basically a hollow container with only a small opening into the mouth cavity, it has been suggested that the cavernous casque functions as a resonance chamber; the theory is that vibrations of the vocal chords are amplified within the casque, along similar principles to those applying to stringed musical instruments, such as the violin. Although *Bycanistes* and *Ceratogymna* hornbills are quite different from the members of other African genera, they are much like the majority of the Asian hornbills. They occupy forest habitats, and they feed mainly on fruit. In particular, they swallow a number of fruits and then carry them in the oesophagus to the nest, where they regurgitate one fruit at a time into the tip of the bill and then pass it to the nest inmates.

The five medium-sized species in the genus *Bycanistes* all have a greater or lesser amount of white on the rump and back, and on the underparts, which is one of the criteria by which they have been separated generically from *Ceratogymna*. The two *Ceratogymna* species are distinctly larger, and with white more or less restricted to the tail, but each has pendulous wattles of naked blue skin that hang below the throat, a criterion that has been used to place them alone in the genus. All species



The number of genera within the Bucerotinae is open to debate, with 8-13 typically designated. One of only three monotypic genera currently recognized belongs to the Long-tailed Hornbill. This aberrant species inhabits the humid forests of West Africa, where it often feeds by catching insects in flight. This unusual foraging technique, along with the ample crest, elongated rectrices and unusual howling call combine to suggest that it lacks close relatives. It is probably most closely allied to the dwarf-hornbills, two miniature members of the genus *Tockus*, with which it shares elements of foraging behaviour and a lack of complex display.

[*Tropicranus albocristatus cassini*, Lekki Peninsula, Nigeria. Photo: A. P. Leventis]



The five species that make up the African genus *Bycanistes* are fairly large forest-dwelling hornbills with impressive casques, the latter especially prominent in males. They resemble the majority of Asian hornbills in their arboreal lifestyles and in being primarily frugivorous. It is possible that more species are involved as, for instance, according to recent genetic analysis, isolated montane populations of the Silvery-cheeked Hornbill are quite distantly related and perhaps deserve species status, although at present they are not even separated as subspecies.

[*Bycanistes brevis*,  
Ngorongoro Crater,  
Tanzania.

Photo: Christophe Ratier/  
NHPA]



of both genera, however, share characteristics that are unique among the hornbills. One is the habit of the male of swallowing mud and forming it into pellets, which are regurgitated to the female for use in sealing the nest entrance. Another is that the juveniles of both sexes have brown feathers on the face, a trait that, in the two large wattled *Ceratogymna* species, extends to brown feathering of the whole head and neck. Further-

more, in the case of the wattled species, the adult female retains the brown head and neck, while only the adult male develops all-black plumage in these areas.

The various behavioural and morphological similarities between these two genera of African forest hornbills could be considered good reasons for combining them in a single genus *Ceratogymna*, and they do indeed appear to be very closely re-

The three members of the Asian genus *Ocyrocus* superficially resemble the African genus *Tockus*, and have clearly diverged relatively recently; indeed, over the years the two genera have usually been merged. The Malabar Grey Hornbill, along with its congeners of the Indian Subcontinent, differ from their African cousins in lacking a complex display, although one species enacts a rudimentary version. Another important difference is the fact that in *Ocyrocus* males provision females and nestlings by regurgitating several items from the gullet, rather than carrying each item individually.

[*Ocyrocus griseus*,  
Periyar Sanctuary, India.  
Photo: Gertrud &  
Helmut Denzau]





The Plain-pouched Hornbill is a poorly known species that has been the subject of considerable taxonomic vacillation. It was long treated as a race of the Papuan Hornbill (*Rhyticeros plicatus*), or even as the juvenile of the Wreathed Hornbill (*Rhyticeros undulatus*). The latter mistake was only corrected when it was found to mate assortatively, even though many specimens in museums are clearly adult, because of their casque structure. It differs in many minor features from the sympatric and generally much commoner Wreathed Hornbill, most notably in the lack of a black bar on the throat pouch and the absence of corrugations on the sides of the mandibles.

[*Rhyticeros subruficollis*, Huai Kha Khaeng Wildlife Sanctuary, Thailand. Photo: Pilai Poonswad/Thailand Hornbill Project]

lated. If that arrangement is adopted, then the differences can be indicated by dividing the species into subgenera.

Whereas there is fairly broad agreement over the systematics of the Bucerotidae within their African range, the situation in Asia appears somewhat more complex. J. L. Peters, in his monumental work on the classification of the world's birds, recognized nine genera of hornbills in Asia, his treatment combining the Indian *Ocyrceros* with the African *Tockus*. This arrangement was rather closely followed in 1960 by K. Sanft and in 1975 by J. J. Morony and colleagues, although both of those works recognized ten Asian genera, including *Rhyticeros*, which Peters had merged with *Aceros*. More recently, A. Kemp preferred to emphasize the close affinities of many of the Asian taxa by dividing the 31 species into just six genera, merging *Ptilolaemus* with *Anorrhinus*, *Rhinoplax* with *Buceros*, *Tropicranus* with *Tockus*, and *Berenicornis* and *Rhyticeros* with *Aceros*, but, importantly, recognizing *Ocyrceros* as a valid taxon. The most obvious effect of this latter approach is that no genera of hornbills have members in both Africa and Asia. While the three *Ocyrceros* species do superficially resemble the small African *Tockus* species and have, traditionally, been united with them, they differ in several fundamental aspects. Most importantly, *Ocyrceros* hornbills do not usually carry food to the nest as a single item in the tip of the bill, but rather, like most other hornbills, they regurgitate multiple items from within the gullet. They also lack any elaborate territorial displays, although one species has a rudimentary display, and another has whistling calls that are reminiscent of those of these birds' counterparts in Africa. All three of the *Ocyrceros* are found relatively close to Africa, in India and Sri Lanka. One of them, the Indian Grey Hornbill (*Ocyrceros birostris*), is the only real savanna-dwelling hornbill in Asia, where all other species live in forest habitats.

The Indian Grey Hornbill also has slightly elongated central tail feathers, a trait shared with several species in the genus *Anthracoeros*. The latter contains five species that are superficially similar to the African species of *Bycanistes* and *Ceratogymna*. They are medium-sized hornbills, with black and

white plumage, and with a large casque, and they feed at the nest by regurgitation. The main difference from the African genera is that the casque of the female is almost as large as that of the male, a fact which makes it difficult to distinguish between the two sexes. In addition, *Anthracoeros* hornbills have no white on the back, unlike *Bycanistes*, and they lack the bare throat wattles of *Ceratogymna*, while the juveniles look just like young adults, without any special brown markings on the face. There are, however, differences between the sexes in the colour of the bill and that of the bare skin around the eye, and, in one species, in the colour of the eye itself. *Anthracoeros* hornbills are spread across a wide area, from western India and through South-east Asia, east to the outlying eastern islands of Sumatra and Borneo. Two of the species, which extend this range even farther east, to the neighbouring Philippine archipelagos of Palawan and Sulu, have distributions that are among the smallest of those of any individual hornbill species.

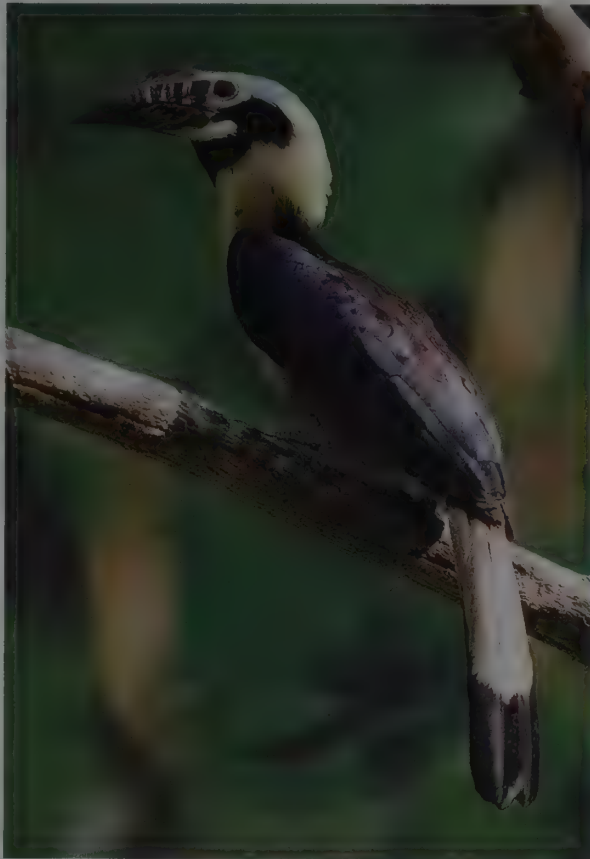
The largest of the Asian hornbills are the three species in the genus *Buceros* and the single species of *Rhinoplax*. They, too, extend across a wide Asian range, from western India to Sumatra, Java, Borneo and the Philippines. Each species has its own form of distinctive large casque and bill, the sizes and structures of which are once again similar for both sexes. The differences among the species in the structure of the casque suggest that this impressive feature is probably used mainly in territorial and sexual display. Most strikingly, the casque and the bill of each species are brightly coloured in red, orange or yellow, not by a pigment in the bill, but by cosmetic application of coloured oils from the preen gland. As with most other birds, the preen gland is situated on the upper side of the base of the tail, but in these hornbills it is especially elaborate, being crowned by a plum-sized tuft of soft feathers. Apparently, the coloured oils are not yet developed in immature birds, which have the bill uncoloured. All of the outside Asian hornbills also have a white tail, with a broad black band across the centre in at least one age-class, and, in addition, the colours of the eye, the casque and the facial skin differ in detail between the sexes and among the age-classes.



Members of the genus *Penelopides* are given the name "tarictic hornbills", as an onomatopoeic echo of their main call. Until recently this genus was considered to contain only two species, one on Sulawesi, the other widespread in the Philippines. After a recent reappraisal, however, the Philippine form has been split into four separate species, and may yet be further subdivided. Two of the resultant species are the Visayan and Mindanao Tarictic Hornbills, the males of which are essentially similar, though that of the former has rufous uppertail-coverts. Details of bill morphology also differ, although both possess the grooved plate-like structure at the base of the mandibles that characterizes all members of the genus.

[Left: *Penelopides panini*, Negros, Philippines. Photo: Juan Cornejo.]

Right: *Penelopides affinis*, Mindanao, Philippines. Photo: Roland Seitre/Bios]



Although the Helmeted Hornbill (*Rhinoplax vigil*) differs from the three *Buceros* species in several aspects, such as its markedly elongated central rectrices, some particularities of its casque structure and its more complex vocalizations, it shares many features with them and is consequently sometimes treated as congeneric.

In the remaining five genera of Asian hornbills, the most constant feature is that the juveniles of both sexes resemble the adult male in the colour of their plumage. In most of these species, juveniles and adult males have the face, head and neck, and sometimes also the belly, coloured brown or white. Only in adult females do these areas become all black at the first moult of the

brown juvenile feathers. The smallest of these genera, *Anorrhinus*, with only three species, is made up of medium-sized hornbills with broad, bushy head feathers. Two brown species occur on the Asian mainland, where they were in the past considered to be only subspecies within the same species, and were generally combined in their own monospecific genus *Ptilolaemus*, a treatment preferred by Peters and, later, by Sanft and by Morony and colleagues. The third species, the Bushy-crested Hornbill (*Anorrhinus galeritus*), occurs in the Sunda region, in an area that comprises the Malay Peninsula and the adjacent islands of Sumatra and Borneo, landmasses that were all linked together during prehistoric periods of lower sea levels and are currently

Jackson's Hornbill was first described as a separate species but later thought to be the immature plumage of Von der Decken's Hornbill because of the spotted wing coverts evident in this photograph. These two forms resemble each other in bare part coloration, vocalizations and behaviour, and they are thus now usually treated as conspecific, although considerable plumage differences suggest that further research is warranted in the likely contact zone in the east Turkana region of Kenya.

[*Tockus deckeni jacksoni*, Nakuru National Park, Kenya. Photo: Jacques Gilliéron]





Despite its considerable size, the hornbill bill can be used surprisingly delicately as a precision instrument, notably in taking hold of small food items. Plumage pigments of hornbills are melanin-based and therefore rather dull. In some Asian species, particularly those in the genus *Aceros*, drab or piebald plumage is strikingly offset by bright bare-part colours on and around the head. The handsome male Knobbed Hornbill, endemic to the island of Sulawesi, provides perhaps the most vivid demonstration of this tendency. Bills in this genus develop slowly and markings are added at regular intervals, typically at the rate of one groove near the base of the mandibles or an extra tier to the casque per annum. This allows the age of individuals to be estimated during the first few years of life.

[*Aceros cassidix*,  
Sulawesi.  
Photo: Tui De Roy]

separated only by shallow seas. All three *Anorrhinus* species have loud cackling calls, and all live in small groups the members of which breed co-operatively. Neither their cackling calls nor their breeding habits are unique among the Bucerotidae, and, so far as is currently known, these species are not otherwise distinctive.

Another genus of hornbills in which the females, in all but one case, have an all-black or all-dark body plumage is *Penelopides*, the five small species of which are known as tarictic hornbills, after an onomatopoeic rendition of the main call of several of them. They are further distinguished by the plate-like structure at the base of the mandibles, ridged with transverse bars as in some larger *Aceros* and *Rhyticeros* species, genera which also have all-black females. The *Penelopides* hornbills have an unusual distribution, occurring on the Indonesian island of Sulawesi and on most of the islands of the Philippine archipelago. The traditional view has been that only one species was present on each of the respective island groups, but a reappraisal of the different populations on the islands of the Philippines suggests that they should be divided into at least four species. The range of the genus is restricted to the Philippines and the region commonly referred to as Wallacea, the interface between the great faunas of Asia and Australasia that was first documented by the eminent naturalist Alfred Russel Wallace.

The final three Asian genera consist of eleven medium-sized to large species, the females of which, yet again, have an all-black body plumage. As a group of rather closely related hornbills, they extend from Nepal and eastern India all the way east to the Philippines, and south, past New Guinea, to the Solomon Islands. The ten species of *Aceros* and *Rhyticeros* are mainly frugivorous, wandering long distances in search of fruiting trees, and often assembling in large flocks at food sources or at roost-sites. This nomadic and social lifestyle seems to have predisposed them to colonize remote and scattered islands. Indeed, *Rhyticeros* is the only bucerotid genus with a species that extends east of Wallacea, into the Australasian faunal region, and with two other species that have evolved independently on the outlying oceanic islands of Narcondam and Sumba.

Because of the similarities in their plumage patterns and in several aspects of their behaviour, among other things, *Aceros* and *Rhyticeros*, along with monospecific *Berenicornis*, have been merged by some authors, notably by Kemp in 1995, who recognized the differences between the three by according them the status of subgenera. The species that are included in these three genera have, in the past, been divided between *Aceros* and at least two other genera. *Aceros* was the name originally used only for the Rufous-necked Hornbill (*Aceros nipalensis*) of the Asian mainland. All but one of the ten other species were either combined in this same genus, *Aceros*, or separated into their own genus, *Rhyticeros*. The species can, in fact, be divided easily by their casque structure into two groups, each of five species, that may be recognized as separate genera or subgenera. Members of one group, *Aceros*, have a tall, wrinkled casque, the simple low casque of the Rufous-necked Hornbill being considered possibly the ancestral form, and all have a long white tail with either a black base or a black tip. They range from the Asian mainland to the eastern limits of Wallacea, on the islands of Sulawesi and the Philippines. The other group, *Rhyticeros*, also occurs on the Asian mainland, but it extends even farther south and east to the outermost islands of Australasia. Its members have a low, wreathed casque and a short, all-white tail, except for the isolated species on the island of Sumba, which has a long, all-black tail.

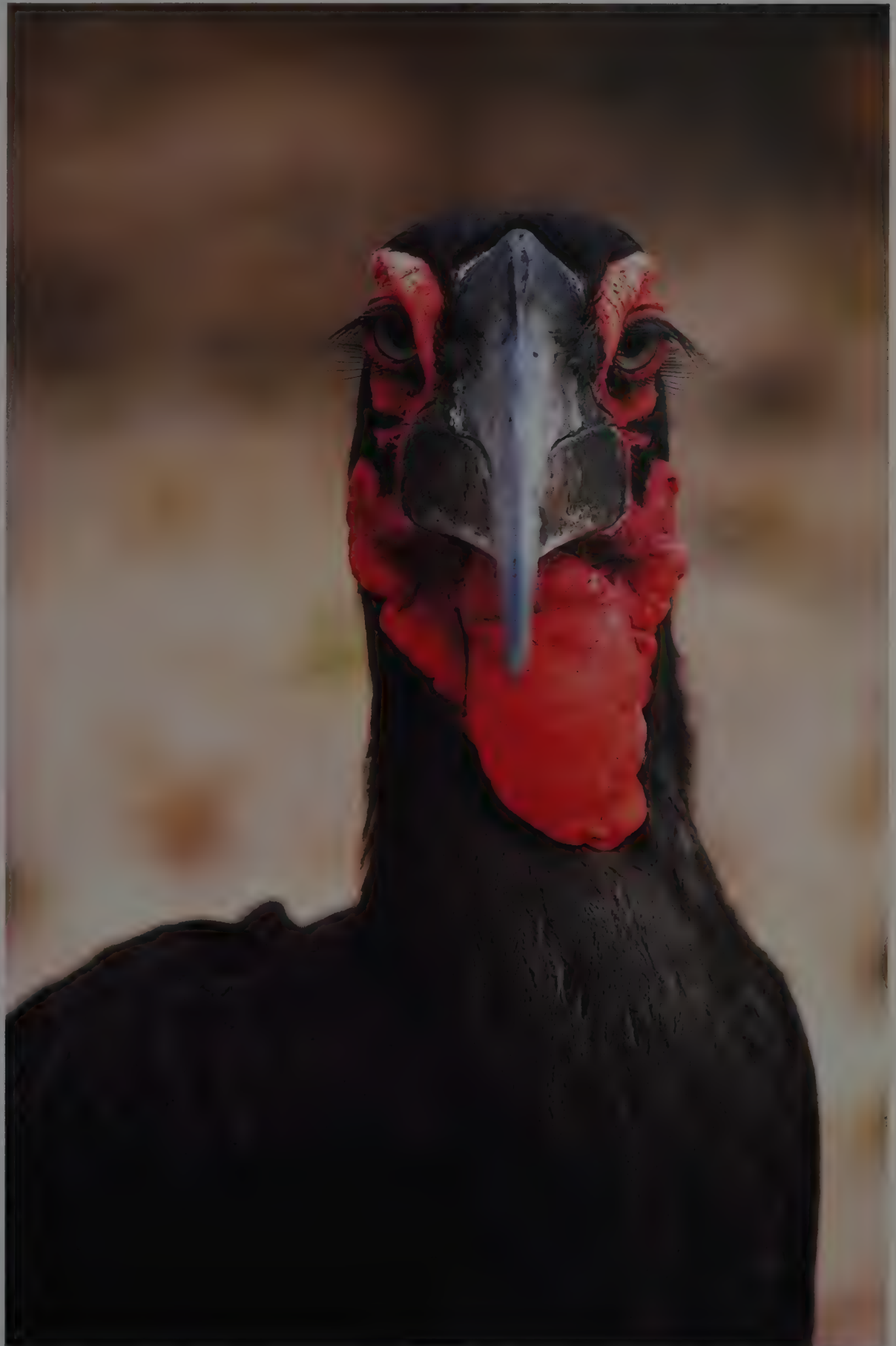
This latter group contains the Plain-pouched Hornbill (*Rhyticeros subruficollis*), the single hornbill species with the most chequered and confused taxonomic history. This situation arose because of its close resemblance to some Wreathed Hornbills (*Rhyticeros undulatus*), and underlies major errors in identification that led in turn to repeated misjudgement of its distribution, a circumstance only recently clarified by P. Rasmussen of the Smithsonian Institution. Since its description by E. Blyth in 1843, the Plain-pouched Hornbill has suffered countless revisions of its taxonomic status that have classed it variously as a full species, as a race of the Papuan Hornbill (*Rhyticeros plicatus*) or even, perplexingly and for a considerable period, as the juvenile of the Wreathed Hornbill. When this form was finally found to



Few avian families span the range of body size shown by the hornbills. The smallest female *Tockus* hornbills weigh less than 100 g while the largest male Southern Ground-hornbills apparently sometimes exceed 6 kg. This species has an inflatable scarlet throat pouch which may function in sound production or status signalling. It also wears what looks like a set of false eyelashes, a feature that accentuates its faintly comical appearance and comportment.

The Bucorvinae are certainly an early offshoot of the hornbills. By plotting genetic differences against standard divergence rates, it can be reckoned that the subfamily separated from the Bucerotinae roughly seven million years ago, an ancient origin that gives rise to a multitude of highly anomalous morphological and behavioural traits and an endemic genus of feather lice. Interestingly, the two ground-hornbills share another genus of feather lice only with the large arboreal Asian hornbills, *Buceros* and *Rhinoplax*. Furthermore, these three disparate genera are the only hornbills known to possess cosmetic preen-gland tufts. While these links are quite possibly coincidental, and there are many morphological inconsistencies to suggest that this is indeed the case, it might be speculated that the ground-hornbills are the last remnant of a group that gave rise to their distant Asian relatives. In many areas, ground-hornbills have become rather rare and reclusive because they are hunted for food, but where they are well protected they can be remarkably tame and inquisitive, as any visitor to the Kruger National Park in South Africa will discover.

[*Bucorvus leadbeateri*,  
Kruger National Park,  
South Africa.  
Photo: Anthony  
Bannister/NHPA]





breed assortatively in the range of the Wreathed Hornbill this last theory was debunked, but the close resemblance of males to juveniles of that species, especially of the Sundaic or northern varieties, led to its being erroneously reported in Sumatra and northern Myanmar. A re-evaluation of specimen records from these areas has revealed that, in all cases, Wreathed Hornbills had been wrongly identified and genuine Plain-pouched Hornbills thus occupied a more restricted range than previously suspected. They are confined to the range of hills separating southern Myanmar from Thailand, with an isolated, long-overlooked, but apparently thriving population in the forests of northern Peninsular Malaysia.

The most aberrant species of Asian hornbill is the White-crowned Hornbill (*Berenicornis comatus*). It has an all-black female, but it differs from all similar species in having virtually no casque, and in possessing a bushy white crest and a long, graduated, white tail. In addition, it leads a sedentary existence and it lives in small groups, the members of which breed co-operatively.



tively. This hornbill has traditionally been placed alone in its own genus, *Berenicornis*, alongside the *Anorrhinus* species, with which it shares the bushy crest and co-operative habits. Another taxonomic treatment has joined it with the Long-tailed Hornbill of Africa in the genus *Tropicranus*, because both species have a white crest and a long, graduated tail. Since the White-crowned Hornbill shares the all-black female plumage with the Asiatic *Aceros* and *Rhyticeros*, it may be better considered to be closer to those, but its exact placement remains uncertain. The little that is known about this species' biology and behaviour indicates that it belongs among the Asian genera, and it seems hardly likely to be affiliated to the genus *Tockus*, to which *Tropicranus* is closely related.

While the relationships between hornbill genera remain uncertain on present information, there is one further line of evidence that does support the current divisions between those genera, and the arrangements within them. This evidence comes from the feather lice (Mallophaga) that live as parasites on the plumage of hornbills. Since the lice spend their entire life on their avian host, and since many louse species are so selective that they are able to survive on only one or a few particular species of hornbill, the relationship between hornbill lice should closely reflect the relationship between the hornbills themselves. Only two genera of hornbills have their own exclusive genera of feather lice, these being the *Bucorvus* ground-hornbills and the *Anorrhinus* bushy-crested hornbills. This exclusiveness indicates that these genera of hornbills diverged from the other bucerotids at an early stage, thereby allowing sufficient time for the lice themselves to evolve into distinctive genera. Such an early separation is supported for the ground-hornbills, on the basis of anatomical and behavioural evidence, and it is suggested for the three *Anorrhinus* species by their lack of any novel features other than the bushy crest.

Other groups of hornbills that are clearly separated in terms of the lice which live on them include the remaining African genera. Thus, the forest-dwelling *Bycanistes* and *Ceratogymna* hornbills are not close to the *Tockus* and *Tropicranus* species of the savanna and woodlands, and, within the genus *Tockus*, the "whistlers" can be separated from the "cluckers". At this stage of our knowledge, the Asian genera are not easily separated by their lice, and the only apparently reasonable proposition that can be made is that the small taretic hornbills in the genus *Penelopides* are closest to the "wrinkled" and "wreathed" groups of large hornbills in *Aceros* and *Rhyticeros*. It is unfortunate that lice have not been recovered from the aberrant White-crowned Hornbill, as these might have helped to resolve its uncertain relationships. Among the Asian genera, it remains to be determined whether the general lack of congruence concerning relationships is referable to the hornbills themselves or to their lice.

An anomaly in the distribution of feather lice is that the two African ground-hornbills share a particular genus of lice (*Bucerophagus*) only with large Asian hornbills in the genera *Buceros* and *Rhinoplax*. In these Asian species, the preen gland has a special tuft that is used to apply coloured oils to the bill and the plumage. Somewhat surprisingly, the ground-hornbills have a similar preen-gland tuft and, although both have a black bill, one species has a small yellow stripe at the base of the bill. Are these African and Asian genera more closely related than would appear to be indicated by other features? An alternative possibility is that the ground-hornbills are the sole remnant of a group that gave rise to large *Buceros* forest hornbills in Asia and to large *Ceratogymna* forest hornbills in Africa.

Until recently, the relationships among the Bucerotidae had not been studied to any great extent by the use of the various modern techniques of molecular biology. A comparison between more traditional analyses of interspecific relationships, using morphological and behavioural characteristics as outlined above, and the results derived from modern molecular or genetic studies, could provide important insights into the evolution of hornbills. This would be especially valuable, because the comparative morphology, the behaviour, the biogeography and the biology of the hornbills have already been described relatively well.

Segments of the genetic material DNA from several different species of hornbill, taken from the nuclei of their red blood

The casque on the bill is a feature unique to hornbills. In its simplest design it forms a thickened ridge and probably serves to strengthen the bill, which must be made of light material and yet resistant to strong pressures. In more developed cases, as in this Rufous Hornbill, the structure can take up to six years to grow. It develops from the keratin covering of the jaw and is usually almost hollow, reinforced internally with bony ridges and rods. In some genera coloured oils are applied by wiping the bill against a special tuft on the preen gland. Although hornbill casques are variable in both form and function, they undoubtedly play a role in sexual signalling and competition.

[*Buceros hydrocorax*, Philippines.  
Photo: Robert Bergerot/Bios]

The smallest hornbill is the dove-sized Red-billed Dwarf-hornbill. It has adapted to life in humid forests where it largely ignores fruit and forages instead on small insects in the dense understorey, sometimes following squirrels or swarms of driver-ants and snapping up the invertebrates they disturb.

[*Tockus camurus*, Mouila, Gabon.  
Photo: Yves-Michel de Viviés]



The larger forest hornbills are most impressive in flight. The approach of a flying individual, like this Great Hornbill, is heralded by an amazing rhythmic whooshing or hammering noise caused by air coursing through primary bases or between two narrowed and stiffened outer primaries during the slow rowing of huge wings. This noise is audible at long range and is usually the first, and often the only, indication that a large hornbill is close by over the canopy of dense forest. As different hornbill species give different flight noises, it might be speculated that some form of signalling system is involved.

[*Buceros bicornis*,  
Khao Yai National Park,  
Thailand.  
Photo: Tim Laman]



cells, have been hybridized and the strength of this bond measured by the temperature required to break it. The evidence obtained, published in 1990 by C. G. Sibley and J. E. Ahlquist, supported the opinion that the hoopoes and the woodhoopoes are the closest relatives of the hornbills. In addition, it supported the existing evidence that the *Bucorvus* ground-hornbills, with a genus of feather lice of their own (*Bucorvellus*) and their lack of nest-sealing behaviour and nest sanitation, are the earliest branch of hornbills. Further, the results of these DNA-DNA hybridization tests indicated that, within Africa, the small *Tockus* hornbills branched off at an early stage from the remaining typical hornbills in the subfamily Bucerotinae, while, within Asia, the *Anorrhinus* bushy-crested species, also with their own genus of feather lice, were the earliest offshoot. Most of these major separations were confirmed by a reanalysis of the data by J. Harshman, at the University of Chicago.

Within the large genus *Tockus*, those species grouped as arboreal "whistlers", which raise the head in display, appeared to have given rise to the terrestrial "cluckers", with a head-down display. Unfortunately, however, the relationships between the other genera of typical hornbills examined were not well resolved. The most interesting result suggested that the large African forest hornbills in the genera *Ceratogymna* and *Bycanistes* may be most closely related to the *Buceros* hornbills of the Asian forest. This finding could perhaps support the hypothesis of an earlier link with the species in the *Buceros-Bucorvus* complex, with their cosmetic preen-gland tufts and shared genus of lice.

The next breakthrough came when scientists at the University of California, at La Jolla, in south-west USA, showed that DNA from within the mitochondria of cells could be amplified from the dried-up remains of tissues within moulted feathers. This meant that, by collecting moulted feathers from hornbills in zoos or in the wild, scientists could obtain tissue by a non-destructive, interference-free method. Utilizing this technique, P. Morin, along with co-workers J. Messier and D. Woodruff, compared 340 base pairs of amino acids from the mitochondrial cytochrome-*b* gene (mtDNA *cyt-b*), using the feathers of ten hornbill species. At the time of going to press, it was learnt that S. Huebner and colleagues, at the Universities of Heidelberg and Ruprecht-Karls, in Germany, had sequenced 934 base pairs of the same gene for 24 hornbill species, using either blood or feathers.

Both those studies of mtDNA *cyt-b* once again strongly supported the separation of the ground-hornbills from the typical

hornbills, not only at the subfamily level, but even to the extent that the two groups appear to represent different families. Moreover, the time of this separation could be estimated, based on the rate at which changes in the sequence of base pairs accumulate in the genes, this rate providing a so-called "molecular clock". This clock indicated that ground-hornbills separated from typical hornbills about seven million years ago. It also suggests that ground-hornbills may have been the earliest form of hornbill, since the only known fossil hornbill is a *Bucorvus* from 15 million years ago. On the other hand, the two surviving species of *Bucorvus*, in north and south-eastern Africa respectively, are estimated to have diverged only about 1.75 million years ago.

Within the "true" hornbills, the small African *Tockus* species were once again shown, by these DNA studies, to be an early offshoot. Their separation into arboreal "whistlers" and terrestrial "cluckers" was also corroborated, but so profound was the



Like other frugivorous species, the Black-casqued Hornbill often travels long distances each day in response to the patchy and irregular availability of fruiting trees in large areas of forest. Frugivory in hornbills is also associated with gregariousness and communal roosting: nocturnal congregations of some species contain literally thousands of individuals. Large flocks often travel to and from such roosts over the same ground at the same time and in the same direction every day, presenting one of the remarkable spectacles of the rainforest.

[*Ceratogymna atrata*,  
Ivory Coast.  
Photo: Roland Seitre/Bios]



Southern Ground-hornbills become airborne only infrequently, but in doing so they reveal the startling white primaries that are usually hidden within the folded wing. The distinctly thickened and elongated tarsi are clearly visible in this photograph.

These, along with the short, robust toes, are undoubtedly adaptations to their terrestrial lifestyle and the task of bearing the weight of such a bulky body.

[*Bucorvus leadbeateri*, Masai Mara, Kenya. Photo: Jonathan Scott/Planet Earth]

genetic measure, using mtDNA *cty-b*, of the differences between those two groups that it appears that they should be placed in separate, new genera. The African *Bycanistes* and *Ceratogymna* were once again shown to be closest to the Asian *Buceros*. The former two genera were combined by Kemp in the single genus *Ceratogymna*, but the two largest species, with pendulous blue throat wattles, were estimated to be so different from the five smaller, white-rumped species that the latter should be returned to their original genus, *Bycanistes*.

The new mtDNA studies offer much more resolution for the Asian genera. Once more, the *Anorrhinus* genus of primitive bushy-crested hornbills emerged as the earliest offshoot. The

small Wallacean species, in the genus *Penelopides*, were shown to be so close to the larger and more widespread *Aceros-Rhyticeros* group that possibly they are even part of, and evolved from, the latter. The two groups are united in that only the adult female develops an all-black head and neck. In combination, the genera *Penelopides* and *Aceros-Rhyticeros* are only distantly related to the *Anthracoceros* hornbills, an unsatisfactory grouping in which the pied species appear to be generically distinct from the Black Hornbill (*Anthracoceros malayanus*). Finally, yet another new relationship is suggested for the aberrant White-crowned Hornbill. The mtDNA technique placed it alongside the *Buceros* hornbills, reasserted that it should be kept in its own genus *Berenicornis*, and hinted that it may also be close to the similarly bushy-crested *Anorrhinus* species.

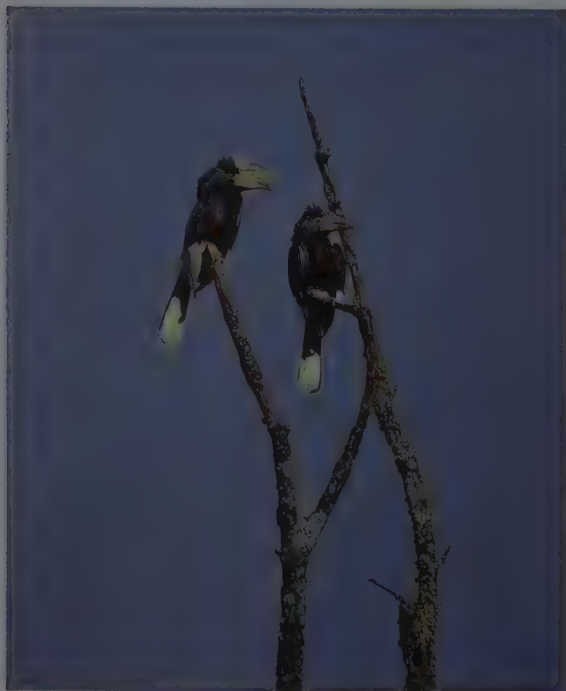
The ultimate surprise came when mtDNA, taken from a number of individuals within a species as part of the overall sample, was found to differ among those individuals to such an extent that the validity of the species' limits was in doubt. Populations of a species that are separated geographically often differ in small but constant details, such as eye colour or bill form, and these differences are usually recognized by naming the distinctive populations as subspecies. A genetic measure of the difference between such subspecies is usually small, so that any larger differences, if detected, would suggest the possibility that the distinctive subspecies in question should be accorded the status of a full and separate species. The genetic studies appear to confirm that the various island populations of the Philippine *Penelopides* hornbills are, indeed, separate species, but such a reassessment is also indicated for at least the Red-billed Hornbill (*Tockus erythrorhynchus*) and the African Grey Hornbill (*Tockus nasutus*), and even for the separate montane populations of the Silvery-checked Hornbill (*Bycanistes brevis*).

Any meaningful conclusions based on molecular studies will become available only when samples have been analysed for all species and subspecies of the Bucerotidae, and when the techniques have been applied to, and compared for, several different parts of the genetic code. Such results are awaited with keen interest, not only for their intrinsic value in research, but also because inaccurate allocation of individuals or populations to species or genus can adversely influence conservation decisions. Inadequate identification of hornbill species can result in genetically

Males of the African genera *Bycanistes* and *Ceratogymna* possess some of the most highly developed casques, whereas their respective females show much more modest versions.

In most cases, the casque is hollow, but there is a small opening at the mouth, so it presumably functions as a resonating chamber, as does the body of a guitar or violin. Resonance of the syringeal membranes could be enhanced by casque design, a circumstance that would explain the impressively far-carrying vocalizations of the Grey-cheeked Hornbill that echo across the African rainforests.

[*Bycanistes subcylindricus subquadratus*, Kakamega, Kenya. Photo: Joe Tobias]





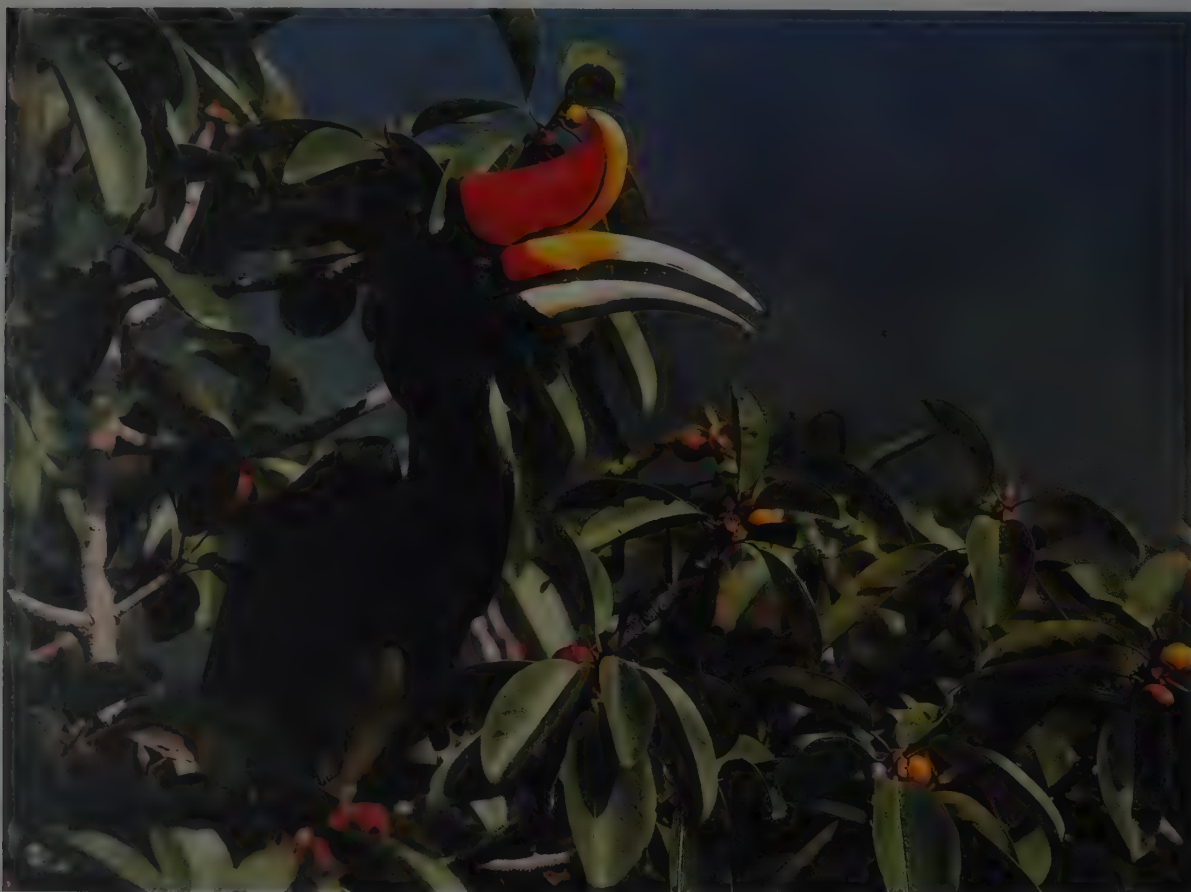
Owing to the distribution of food and suitable nest-sites, hornbills are mostly forest birds. This is certainly the case in Asia where of 31 species, all but one live in or at the fringes of humid forest. The Oriental Pied Hornbill, here seen perching on a huge dead tree in Thailand, is a relatively widespread species that tolerates degraded or patchy forest habitat. Some species are more reliant on intact tall forest and all are constrained to some extent by the presence of large trees in which their nest cavities can be found. A relatively high proportion of Asian species (15/31; 48%) are restricted to islands, where they are highly susceptible to forest loss because of their relatively small ranges. Most Asian hornbills are lowland species, with only one restricted to the montane zone. The proportion of humid forest hornbills is lower in sub-Saharan Africa, reflecting the greater availability of low stature dry forests, scrub and semi-desert. Of 23 species found there, 13 (57%) frequent deciduous woodland or savanna. Humid-forest hornbills belong to the genera *Tropicranus*, *Bycanistes* (like the Piping Hornbill shown here) and *Ceratogymna*, with the two dwarf-hornbills in the genus *Tockus* also restricted to forest. All these species are distributed within the Lower and Upper Guinea forests of West Africa, the Congo Basin and montane or coastal forests of East Africa.

[Above: *Anthracoceros albirostris albirostris*, Khao Yai National Park, Thailand. Photo: Art Wolfe]

Below: *Bycanistes fistulator duboisi*, River Epulu, Ituri, Zaire. Photo: Bruce Davidson/BBC Natural History Unit]







Amongst the most spectacular and remarkable members of the family is the Rhinoceros Hornbill, aptly named because of its horn-like casque. This species is restricted to relatively intact rainforest in the Malay Peninsula and the Greater Sundas, where it forages widely on fruit. In Borneo, it is something of a mythical creature in local traditions. Although it is not sacred inasmuch as it has always been a favoured target for tribal hunters, its casque nevertheless ornaments many canoes, tools and long-houses, its tail feathers adorn the capes of tribal dancers, and the Iban of Sarawak carve wooden Rhinoceros Hornbills as the central theme of their martial rituals.

[*Buceros rhinoceros borneoensis*, Gunung Palung National Park, West Kalimantan, Borneo. Photo: Tim Laman]

distinctive populations being overlooked completely, or even disregarded as being no more than subspecies. Indeed, this is the case for Tickell's Brown Hornbill (*Anorrhinus tickelli*), which is not included in the Asian Red Data book because it is treated as conspecific with Austen's Brown Hornbill (*Anorrhinus austeni*), and the two together are consigned to the lower category of Near-threatened. It can also cause improper matches to be made for conservation management or captive-breeding, as has happened in the case of some Red-billed Hornbills and the Philippine tarictic hornbills, the latter having often been lumped under the name "*Penelopides panini*".

## Morphological Aspects

Very few avian families exhibit the same wide range of body size as can be seen in the hornbills. Females of the smallest dwarf species in the African rainforest can weigh under 100 g, whereas the largest ground-hornbills out on the savanna can weigh well over 4 kg. Since many aspects of the biology of a species can be predicted from their correlation with body size, this also means that the members of the Bucerotidae exhibit, among other features, a wide range of territory sizes, egg sizes, incubation and nestling periods, food requirements and metabolic demands.

Within the hornbills, the other feature related to size is that, in any given species, the male is always larger than the female. The extent of the difference varies among species, being about 1-17% in terms of body mass. The degree of sexual dimorphism also varies for different parts of the body; for example, it is 1-21% for the wing length, but as much as 8-30% for the bill length, since the male's bill is proportionately often much larger than that of the female. The bill and casque of the juvenile are always especially small and undeveloped at fledging, and the juvenile's bill remains slightly smaller than that of adults of the same sex for up to five years, the period of immaturity depending on the size of the species.

The plumage appears rather coarse, hair-like and loose over the body, neck and head. Moreover, the feathers of the head and neck are often erected in display, so that, in many species, they form a fuzzy halo, a loose crest or even an erect crown. The feathers of the abdomen and vent are also rather loose and fluffy. The upperwing-coverts are formed with the normal tight feathering and, although the underwing-coverts are absent, the flight-feathers and the tail feathers are broad and stiff, with thick shafts and strong webbing. The eyelashes are notably well developed, especially in the case of the ground-hornbills, where they are also dorso-ventrally flattened. The tarsus is short and stout, but the toes, both back and front, are rather long, covered in strong broad scales and with wide soles. Once again, the exceptions are the ground-hornbills. These two species have the hind limb elongated, with a thick long tarsus and rather short toes; they extend their stride even farther by walking on only the tip of the hind toe and the anterior parts of the front toes.

In contrast to some of their relatives, such as the rollers, the bee-eaters and the kingfishers, the Bucerotidae do not have any brightly colourful pigments in the plumage. The predominant colours of hornbills are derived from melanin pigments, or the lack thereof, being black, white or some intermediate shade of grey, brown or cream. In many bucerotids the colours are presented as bold patches and markings, but a few species exhibit more delicate marking and shading, or the presence of a green gloss over the black feathers. Where the markings are bold and contrasting, they produce distinctive patterns that are characteristic for each species, especially in flight.

What the plumage of a hornbill lacks in bright colours is made up for by the bare parts, which reveal a variety of bright and gaudy hues. The large bill, the casque that surmounts it, the bare skin around the eyes, the naked throat, the eyelids or the eyes themselves can be coloured red, orange, yellow, blue, green, brown, black or white. The colours are sometimes displayed as large solid areas, or can be in intricate patterns. On the bill and casque the patterns can be enhanced by a series of ridges or grooves, while on the throat they can be presented as small



Most species in the genus *Tockus* are adapted to dry environments, including deciduous woodland, Acacia-dominated savanna forests, and semi-desert. Of these, Monteiro's Hornbill occupies the drier end of the spectrum, inhabiting thornbush savanna and stony hills of the Namib Desert, and even wandering out across level sandy flats when searching for food during dry periods. Although it uses tree-holes for nest cavities, when available, it is more frequently forced to use natural cavities in rocky outcrops, as in this case. In these dry areas there is often no mud to seal the cavity and so the enterprising birds must perform the same task with droppings and food remains.

[*Tockus monteiri*,  
Daan Viljoen Game  
Reserve, Namibia.  
Photo: Christian  
Boix-Hinzen]



patches of wrinkled skin or, in some species, cover the whole of a taut, inflated pouch. The colours of different areas, various organs and the adjacent plumage can blend into one another, or they can be juxtaposed in patches of striking contrast and garish combination.

The colours of the plumage and bare parts, together with the size of the bill and the development of the casque, also indicate the age and sex of an individual. For all species of hornbill, the male and the female can be distinguished, although these external sexual differences can be either slight or extreme, depending on the species. Newly fledged juvenile hornbills can always be recognized by the small bill and the lack of a casque, and these differences, although they diminish as the young bird grows and develops, are useful for a year or more, the duration of such immature characters again being dependent on the species. In some of the larger hornbills, the *Rhyticeros* species being a good example, the casque apparently develops additional tiers at regular intervals, thus allowing the age of individuals to be estimated, at least for the first few years of life. Distinguishing the sex of juveniles on the basis of plumage and bare-part colours, however, is often more difficult and can lead to confusion. Juveniles of both sexes can resemble either the adult male or the adult female, or, less frequently, the juvenile is similar to the adult of the respective sex or is unlike either of the adults of its species. For example, juveniles of both sexes resemble adult males in some *Tockus* species and in almost all *Penelopides*, *Aceros* and *Rhyticeros* species, yet in *Bycanistes* and *Ceratogymna* species they are much closer to the adult female in appearance. It is interesting to note that, while in the *Aceros* and *Penelopides* species the juveniles resemble the adult male, and it is only the females that become all black when adult, the opposite occurs in *Ceratogymna* species, where the juveniles resemble the adult female and it is the males that become all black when mature. In at least two *Penelopides*, a few *Tockus* and one *Bucorvus* species, the juvenile resembles the adult of its respective sex, while in the White-crowned Hornbill, and especially in the Rufous Hornbill (*Buceros hydrocorax*), the juvenile is quite different from either adult.

Hornbills are relatively conservative in the form of their body, wings and tail. The body is small, light and wiry compared with the relatively large, broad wings and long tail. The main exceptions to this basic pattern are those species with a short, square tail, such as the *Rhyticeros* "wreathed" group, or with a long, graduated tail, such as the Indian Grey, the Long-tailed or the White-crowned Hornbills. Some of the small species of *Tockus* and *Ocyrceros* have wings that are rather short and rounded, while in others they are longer and more tapered.

The most diverse and, in most species, the most striking developments and structures are on the head and neck. The large bill varies among species, from being relatively short and deep to being long and slender. It is always decurved in shape, but the degree of curvature varies, so that some species have a relatively straight bill whereas others possess a well-curved bill. The sides of the bill are smooth or have a series of ridges across the base, and the inner cutting edges are either smooth or heavily serrated. The bill is also deeper than it is wide, at least at the base, and the flat sides provide the trowel-like surface that is used to apply sealing material to the nest entrance. Sealing is performed by using droppings, mud or sticky food remains, which are held in the bill while its sides are vibrated against the entrance, either one side at a time or, if the edges of the nesting cavity are close together, in a side-to-side movement. The sealing materials are then squeezed out between the tomia of the bill and plastered on to the entrance rim. The exact application of the sealant is controlled by changing the portion of the bill used in the process, from the fine tip to the broader base, and by altering the angle at which the head is held in relation to the nest entrance.

The casque on the top of the bill is a structure that is unique to the hornbills, and one which shows a diversity of forms among the members of the family. The simplest structure is a low ridge running almost to the tip of the bill, which may serve to reinforce such a long curved blade when strong biting forces are conveyed to the tip by the jaw muscles. The casque is always no more than slightly developed on the smaller, shorter bill of the juvenile. In





Members of the genus *Bucorvus* do not spend all their time on the ground, as this photograph of a Northern Ground-hornbill attests. Nocturnal roosting takes place in trees, with individuals sometimes calling or even descending for a brief walk about when the moon is full. In addition, the birds will fly up into trees to escape danger, when alarmed. The bill and neck of this species are somewhat longer and slenderer than those of its southern relative, presumably underlying some differences in foraging behaviour.

[*Bucorvus abyssinicus*, W National Park, Niger. Photo: Jacques Gilliéron]

larger species with a large casque, the development of this huge appendage may take up to six years to be completed. There are always some sexual differences in the bill and casque of adults, either in form or colour or in both, these ranging from slight to very marked.

In the majority of species with a large casque, the casque develops as a hollow structure from the outer keratin covering of the jaw. It is supported internally by bony ridges and rods, so that, in its most extreme form, as on males of the two *Ceratogymna* species, it becomes a large hollow cylinder. The casque usually

has some small opening to the mouth, and the structure is such that it may function as a resonating chamber, in accordance with Helmholtz's laws. Resonance of the syringeal membranes could be enhanced by resonance of the casque, and this could perhaps account for the loud nasal calls of several large hornbill species. In the ground-hornbills and some *Aceros* and *Rhyticeros* hornbills, which have a small casque, the inflated throat may also have a role in vocal enhancement. Clearly, so large and prominent a structure as the casque can have multiple functions, the most obvious of which, given the sexual differences in the casque's size, col-



Many hornbills are gregarious, with small flocks regularly gathering at food sources and larger flocks, sometimes containing thousands of individuals, recorded at the roost-sites of some frugivorous species. One of the most widespread forest hornbills in Asia is the Wreathed Hornbill. In localities as far flung as Meru Betiri National Park in Java, Kerinci-Seblat National Park in the highlands of Sumatra, Khao Yai National Park in Thailand and Namdapha National Park in India this is the most frequently encountered hornbill, often seen in cackling and rustling congregations in the crown of a fruiting fig tree, or flying in sedate skeins overhead between roosting and foraging sites.

[*Rhyticeros undulatus*, Khao Yai National Park, Thailand. Photo: Pilai Poonswad/Thailand Hornbill Project]



our and details of structure, is probably in competition between members of the same sex or in recognition of potential mates of the opposite sex.

The most bizarre casque is that of the Helmeted Hornbill. In this species, the bill is rather short, stout and straight, but there is a high casque ridge that ends abruptly half-way down the bill in a block of solid ivory. This makes the bill so heavy that the whole skull, including the covering of the bill and casque, comprises at least 10% of the total body weight. The bony supports for this heavy casque, and the muscle attachments enabling the bird to wield the head and bill, are also especially well developed. The function of such a robust bill and casque remains obscure, but these remarkable pieces of apparatus are known to be used in aerial casque-butting contests between rival males. In addition, the bill serves well to chisel off bark, and the mass of the casque may increase the bill's momentum, like a weighted digging stick. It is also of note that both the bill and the casque are brightly coloured with red cosmetic preen-gland oils.

Most hornbills fly with rather slow, deep wingbeats, usually interspersed with short periods of gliding. Among some of the smaller species of the genus *Tockus*, those "whistlers" with exceptionally long, broad wings, such as the African Grey Hornbill, proceed with a buoyant, floating flight. In contrast, the "cluckers", such as the Red-billed Hornbill, have relatively short and rounded wings, which they flap at a rather fast rate, gliding between bouts of flapping, and proceeding with a direct and undulating flight. In the Indian Grey Hornbill, the wings are so short, and the bird flies with such fast beats and so little gliding, that the species is reminiscent of a parakeet (*Psittacula*). These and other aspects of the flight abilities of bucerotids are the result of differences in the lengths and proportions of various wing bones and feathers. They are probably reflected also in differences in flight speed and energetic efficiency.

In many of the larger species, the wingbeats produce a loud whooshing noise, audible to humans at over a kilometre, and with species-specific differences in the exact details of the sound. This appears to be produced by air rushing through either the base of the flight-feathers, which lack underwing-coverts, or through the two small, stiff outer primaries, the tips of

which, in most of the large species, are specially narrowed and emarginated.

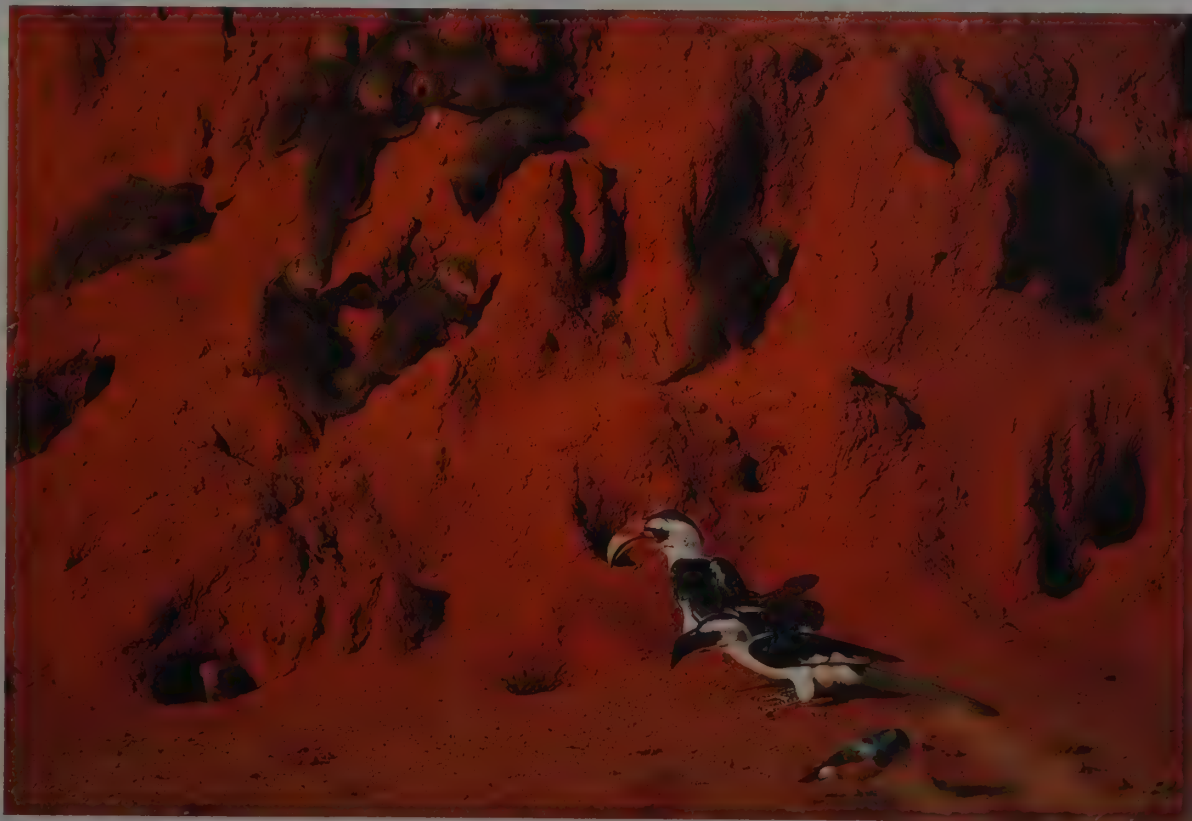
On the ground, and sometimes among large branches, the majority of typical hornbills progress by long hops, executed with both feet together. It is only some of the smaller species of *Tockus* hornbills, those "cluckers" with relatively longer tarsi, that progress by walking and running. As would be expected, the large ground-hornbills of the subfamily Bucervinae, with their proportionately longer legs, also walk and run on the ground. They are, moreover, the only hornbills that scratch the head directly, bringing the foot straight to the head, rather than, as all other hornbills, swinging the leg indirectly behind the wing.

At least in the case of some juvenile hornbills, the moult starts with a change of body feathers a few months after leaving the nest. Although this is not obvious in most species, it can be predicted to occur in synchrony with changes in bare-part colours or casque development that signal changes of age or sexual maturity. This post-juvenile body moult can be observed most readily in juveniles of most *Aceros*, *Rhyticeros* and *Ceratogymna* hornbills. In these species, one sex, the female or male respectively, changes the brown or cream feathers of the head and neck for all-black ones.

As is typical of most avian species, the moult of non-breeding hornbills, as well as that of breeding males, involves a gradual and sequential replacement of the feathers. A detailed study of moult, however, has not been carried out on any bucerotid species, so that, although it is well known that hornbills possess ten primary, twelve secondary and ten tail feathers, the exact sequence in which they replace these feathers is unrecorded for most species. In those cases where it is known, the tail is usually moulted in the sequence T1 or T5 followed by T2 or T4 and, finally, T3, while the primaries start at the outermost P10, with a second moult centre beginning at P3 or P4. The equivalent feathers on each side of the body are not usually moulted together, especially in the tail. Indeed, for the Helmeted Hornbill, a delay of almost a year has been reported between the renewal of the first of the two elongated central tail feathers and that of the second. Alternating moult with a shorter interval has, however, been recorded for several other hornbills, as well as for their nearest relatives, the hoopoes and the woodhoopoes. In some of the bigger hornbill

Associations between hornbills and mammals are not infrequent. One such case involves Von der Decken's Hornbill and the Dwarf Mongoose (*Helogale undulata*), which shelters in termitaria in the arid East African savanna. The relationship has developed in some areas to the extent that hornbills call down termitarium chimneys to summon slumbering mongooses in the morning, whilst, if the birds are late, the mongooses apparently wait for them before setting out to forage. There is presumably a mutual benefit in terms of foraging efficiency: mongooses disturb extra insects for the hornbills, while the hornbills provide increased vigilance, allowing the mammals more time to feed.

[*Tockus deckeni deckeni*, Kenya.  
Photo: Bruce Davidson/  
BBC Natural History Unit]



species, moult of all the larger feathers may not be completed within a year, and in such cases several overlapping waves of moult can then be evident along the flight-feathers. Breeding males may suspend the moult while involved in nesting, presumably because of other energetic demands, but they then resume moult once the chicks have fledged.

Studies of moult in hornbills have focused mainly on what happens to the breeding female while she is sealed up in the nest. In most species, the female completes an almost simultaneous moult of her main large wing and tail feathers, the remiges and rectrices, within a few days of laying the first egg of the clutch. Usually the tail is moulted first, followed by the wings, but the female does not become naked as is claimed in some older references. The moult does, however, render the female incapable of flight, so that, if something happens to her mate or group that prevents them from bringing food to the nest, she will usually starve, even if she breaks out of the sealed nest in an attempt to survive (see Breeding).

Body moult by the female does occur during breeding, but it appears to be slow and gradual. When the onset of breeding is delayed, females of several species are known to start a normal, gradual moult of the flight-feathers, but then to drop only the remaining old feathers if nesting is undertaken. Some individual females, especially among larger species, appear not to attempt a simultaneous moult while breeding, but further details are lacking. These non-moulting females are then able to break out of the nest at any stage of the nesting cycle, for instance if the food supplies fail or if the nest is usurped by competitors. Most females emerge from the nest only once the flight-feathers are virtually regrown, either midway through the nestling period or at the end of that period, when the chicks fledge, the precise timing being dependent on the species.

The hornbills are unusual among birds in that an obligate moult of the major feathers by the female overlaps with egg production and the rearing of the chicks, thereby imposing additional demands and an even greater requirement for nutrients. Furthermore, even

though the male is often the main or the sole provider of food during this period, he may also moult his own feathers at that time.

### Habitat

While hornbills are mostly birds of forest, the habitats which the various species occupy extend from the arid periphery of the Namib Desert in south-west Africa to the tall rainforest of West Africa and South-east Asia. The majority of hornbills are sedentary species, either resident within a small area of habitat or wandering locally, at most over tens of kilometres, in search of fluctuating habitat resources. No members of the family undertake any major migratory movements, and, since the majority of species breed in the cavities of trees that occur within the habitat of their choice, there are also no special movements associated with breeding habitat (see Movements).

Of the 23 hornbill species found in sub-Saharan Africa, a total of 13, or 57%, lives in deciduous woodland or savanna, with the remainder in evergreen forest. India and South-east Asia have only one species, the Indian Grey Hornbill, inhabiting open savanna; the remaining 30 species live in forest habitat, and most of those are confined to evergreen rainforest. These intercontinental differences reflect the approximate extents of savanna and forest in the two regions.

Within the deciduous woodland and savanna habitats of Africa, there are also several basic patterns in the distribution of species and subspecies that are repeated. In the more widespread species, such as the African Grey and Red-billed Hornbills, distinct subspecies can be found on either side of the belt of tall *Brachystegia* or miombo woodland that stretches across central Africa from southern Angola, through Zambia and Malawi, to Mozambique and southern Tanzania. In other instances, two closely related species are confined to one or the other side of the woodland belt, as is the case with the Southern Yellow-billed (*Tockus leucomelas*) and Eastern Yellow-billed Hornbills (*Tockus*



Hornbills are diurnal birds, often roosting at regular sites in the outer branches of trees, or tight against their trunks. They emerge from roosts at, or slightly before, first light and often spend the first few minutes of the day preening and calling. Thenceforth, foraging is discontinued periodically throughout the day to allow for rest or comfort behaviour, most frequently preening. As shown by this Red-billed Hornbill, the length of the bill is an advantage when grooming wing and tail feathers, though it causes problems when the breast or mantle feathers need attention; at these times the hornbill must perform various contortions, so that it can reach the offending plumage. Pair and group members often enjoy prolonged sessions of allopreening, although whether these have any social function is unknown.

[*Tockus erythrorhynchus erythrorhynchus*, Samburu Game Reserve, Kenya.

Photo: Mike Wilkes/  
BBC Natural History Unit]



Hornbills frequently sunbathe, bathe in the rain, or dry their feathers after getting wet.

The *Buceros* hornbills, in particular, regularly respond to sunshine by striking bizarre postures to maximize the sun's effect.

This Rhinoceros Hornbill, for example, is spreading its wings fully, tilting its tail towards the sun and letting its head loll slightly to the side. When hornbills sunbathe, the back faces the sun, the head and rump feathers are usually raised and the wings

are drooped or spread to expose the mantle and uncover the wing plumage. Many species prefer to perform this behaviour on the ground,

as shown by this Red-billed Hornbill. Other poses are adopted so that heat can be lost:

for example, the bill is gaped so that moisture evaporates and cools the air travelling to the lungs.

It is possible that heat may also be lost through the bare gular skin, this potentially being inflated to increase its surface area when required. Other

types of behaviour occur that have no obvious function. These include

toying with sticks, tossing leaves or debris, bill-wrestling or jumping on or over each other.

This type of behaviour is seen most often in juveniles, particularly in co-operative species, and has been termed "play".



[Above: *Buceros rhinoceros borneoensis*, Gunung Palung National Park, West Kalimantan, Borneo.

Photo: Tim Laman.

Below: *Tockus erythrorhynchus rufirostris*, Kruger National Park, South Africa.

Photo: P. Heard/FLPA]





All hornbills have loud vocalizations that they use frequently, partly because calls are important for communicating in densely vegetated habitat, and also because many species have large territories or rove over extensive areas, in both cases requiring signals to be detectable from long range. Most calls are easily distinguishable between species.

The Crowned Hornbill has a loud whistling call that is given by both members of the pair in tandem with a rudimentary display: the raising of the head when calling.

[*Tockus alboterminatus*,  
Aberdare National Park,  
Kenya.

Photo: Dave Richards]

*flavivirostris*). At the southern and northern extremes, and in the most arid savanna habitats occupied by any hornbill, there are such species as Monteiro's Hornbill (*Tockus monteiri*) and Bradfield's Hornbill (*Tockus bradfieldi*) in the Namibian region and Hemprich's Hornbill (*Tockus hemprichii*) in the Ethiopian region. To round off these patterns, the miombo woodland of central Africa has its own endemic species, the Pale-billed Hornbill (*Tockus pallidirostris*). This species occurs in separate subspecies on each side of the Luangwa Valley system of Zambia, a watercourse that is thought to have existed as an arid corridor for the hornbills of more open savanna that occur on either side of it. Such a corridor is proposed to have existed prehistorically, when increased glaciation at the poles caused drier and cooler conditions, with lower rainfall, over most of Africa.

The African hornbills of forest habitats are also divided into species or subspecies that now live in what must have been separate blocks of forest during drier glacial periods. The main block of lowland forest is the vast area of the Congo basin, generally referred to as the Lower Guinea forest. The Upper Guinea forest in West Africa exists as two smaller blocks, one extending from Cameroon and the River Niger to the so-called Dahomey Gap at Togo and Benin, and the other from the Dahomey Gap westwards to Senegal. Both of the Upper Guinea blocks support, among others, the endemic Yellow-casqued Hornbill (*Ceratogymna elata*) and the nominate subspecies of the Brown-cheeked Hornbill (*Bycanistes cylindricus*). Around the edges of the main forest blocks, one species, the Grey-cheeked Hornbill (*Bycanistes subcylindricus*), occupies mainly the ecotone between forest and deciduous woodland. Another bucerotid, the Silvery-cheeked Hornbill, utilizes montane and coastal forest to the east, and a third, the Trumpeter Hornbill (*Bycanistes bucinator*), extends from coastal forest into riverine and hill forest to the south and east.

Most of the Asian bucerotids tolerate a range of forest types and conditions, and in this region the geographical divisions between species are a result largely of the division of habitats into separate islands. Twenty of the 30 Asian hornbills are insular species, and each one occupies whatever forest habitats are available on its particular island. Species with wider ranges are found mainly on the Asian mainland, or extend to adjacent islands which,

at times of low sea-level during the drier glacial periods, were connected to the mainland. The islands of Sumatra, Java and Borneo, which stand on the Sunda Shelf and are currently separated from the Malay Peninsula by only shallow seas, are the prime example. Each of those land areas now supports populations of one or more of four species, namely, the Bushy-crested, Great (*Buceros bicornis*), Rhinoceros (*Buceros rhinoceros*) and White-crowned Hornbills. Other, more widespread species show preferences for forest at different altitudes, as exemplified by the Rufous-necked Hornbill in the hill forest, the Helmeted Hornbill among the foothills, or the Wrinkled Hornbill (*Aceros corrugatus*) in the lowlands. Only a few species have restricted ranges on the mainland. The latter appear either to be the result of constraints imposed by past habitat contractions, as in the case of the Malabar Grey Hornbill (*Ocyeros griseus*), or to be due to special habitat preferences that are poorly understood, a factor which seems to apply to Tickell's Brown Hornbill and the Plain-pouched Hornbill.

Although the hornbill species, collectively, occupy a wide range of either forest or savanna habitats, it should be emphasized that each particular species co-exists with, and relies upon, its own special combination of plants and other animals. This combination varies not only from one area to another, but also from one season to another. The savannas of Africa, for example, are especially rich in small animals, while the forested areas of Asia have a high proportion of fruits with nutritious fatty pericarps, in particular those in the family Lauraceae. Both regions harbour many species of fig tree (*Ficus*), the fruits of which are important to many hornbill species because of their high moisture content and, in some cases, their unexpectedly high calcium content. Figs, however, are more important in Asia than in Africa, while only the latter continent has the rich fruits of the indigenous oil palm (*Elaeis guineensis*), although these palms are now grown widely as a plantation crop in Asia. Depending on regional and seasonal differences in such climatic factors as rainfall and temperature, the fruit crops on trees or the abundance of animal food can be either highly seasonal or rather erratic. The climatic effect is greatest in the savanna habitats of Africa, with their alternating wet and dry seasons, or in the semi-deciduous forest of India and South-east Asia, which experience an an-



The Southern Ground-hornbill lives in sedentary co-operative territorial groups, usually consisting of a dominant pair with accompanying offspring which remain with their parents well into maturity and contribute to the provisioning of nestlings. Groups of up to 11 birds have been recorded, although it is unsure whether all these were descendants of the dominant pair. All individuals contribute to the defence of an all-purpose territory of variable size (2-100 km<sup>2</sup>). The size of this territory is necessarily extensive as ground-hornbills require an abundance of food and, being carnivorous, this is usually distributed thinly throughout the habitat. They give deep booming cries before first light and periodically through the day. In the pre-dawn stillness, when the savanna air is cool, ground-hornbill booms can be heard by people over 5 km away and are then sometimes mistaken for the low groaning of lions. In addition to vocalizations, ground-hornbills perform other, more sophisticated displays. Mandibulating an egg with care, for example, is part of the dominance display acted out by the dominant pair in front of other members of the breeding group. This also serves us as a reminder of the versatility of the hornbill bill. Although the mandibles of this species are used like a pickaxe to dispatch living creatures up to the size of a hare and are capable of heavy-duty bone-crushing, skull-cracking, seed-breaking and soil-digging, they can also be used delicately to carry fragile objects.

[*Bucorvus leadbeateri*.

Above: Tsavo East National Park, Kenya. Photo: Bruce Davidson/ BBC Natural History Unit.

Below: Kruger National Park, South Africa. Photo: Nigel J. Dennis/ NHPA]





A minority of hornbill species conduct a ritualized form of display, and the bulk of these are in the genus *Tockus*. Pairs of Southern Yellow-billed Hornbills, for example, cluck and cackle loudly, always with their heads bowed, their wings raised and their tails spread. This display is almost identical to that of two other closely related species, the Eastern Yellow-billed Hornbill (*Tockus leucomelas*) and Von der Decken's Hornbill (*Tockus deckeni*), although morphological variation, principally in bill colour, ensures that different signals are conveyed. Other *Tockus* species have analogous stylized behaviour, but some only call with their heads raised, and some never fan their wings or tails. The calls given by most *Tockus* hornbills are divided between the "cluckers" and the "whistlers", and there is some molecular evidence that deeper genetic differences underlie this vocal pattern. There are some odd similarities between the displays of distantly related hornbills, such as the raised tail fanning at the end of each display adopted by Hemprich's Hornbill (*Tockus hemprichii*) of Africa and the Rufous-necked Hornbill (*Aceros nipalensis*) of Asia.



[*Tockus leucomelas*, Kruger National Park, South Africa. Photos: Hanne & Jens Eriksen/BBC Natural History Unit (above); Hanne & Jens Eriksen (below)]



nual monsoon season. Fluctuations of those types are quite different from the regular monthly temperature and rainfall patterns of the tropical rainforest.

The requirements of each hornbill species also differ. One may feed on many species of insect, whereas another may feed on fruit from at least a hundred different plant species (see Food and Feeding). Each hornbill species has a variety of ways of collecting this food, and will have an impact on each type of food either as a predator or as a dispersal agent. Once again, regional trends emerge. It is only in Africa that several bucerotids are reported to associate with other animals, ranging from ants and monkeys to mongooses and chanting-goshawks (*Melierax*), to take advantage of the prey which those animals disturb, while in Asia only a few hornbill species seem to interact, occasionally, with hawk-eagles of the genus *Spizaetus* (see Food and Feeding). The choice of nesting tree will also differ from one habitat to another, depending both on the size and structure of each tree species and on the agents that will create the cavities used for the nest. In Africa, feeding elephants are important agents in that they break off tree limbs, thereby starting the formation of nesting cavities. In Asia, the holes made in tree trunks by bears as they search for honey are similarly a major factor.

### General Habits

Hornbills are diurnal birds, and most begin their day at first light. Often, they emerge from the roost to perch in the open for a while, preening or calling, before they move off to forage. Those which feed on evenly dispersed food sources, such as insects, can begin to feed from the moment they leave the roost, and continue feeding as they move about during the day. Other species which feed at patchy food sources, such as fruiting trees, may have to fly long distances before they can start to feed, and they then have to spend periods during the day in moving between different feeding sites.

Usually, hornbills move around in pairs or, after the breeding season, in small family groups. Compared with most other families of birds, however, the Bucerotidae contain more species that live as co-operative groups, these containing up to 20 individuals, depending on the species in question. Each group consists of a dominant pair of breeding adults that is assisted by adult and juvenile helpers. The helpers take part in the defence of the territory, the delivery of lining material to the nest-site, and the provision of food to the breeding female and chicks. Co-operative breeding (see Breeding) has been confirmed for at least eight species of hornbill, and is suspected for a further ten, these totals corresponding to 15% or, possibly, even 33% of all hornbill species. The members of each co-operative group are assumed to be closely related, often offspring of the dominant pair, although this has not been tested for any hornbill species. In those species that have been studied, there appears to be a predominance of adult males in each group and in the population as a whole. Again it is assumed that, as for many other co-operative bird species, it is the males that tend to remain within the parental group and territory, while the adult females tend to move between groups in search of new breeding opportunities.

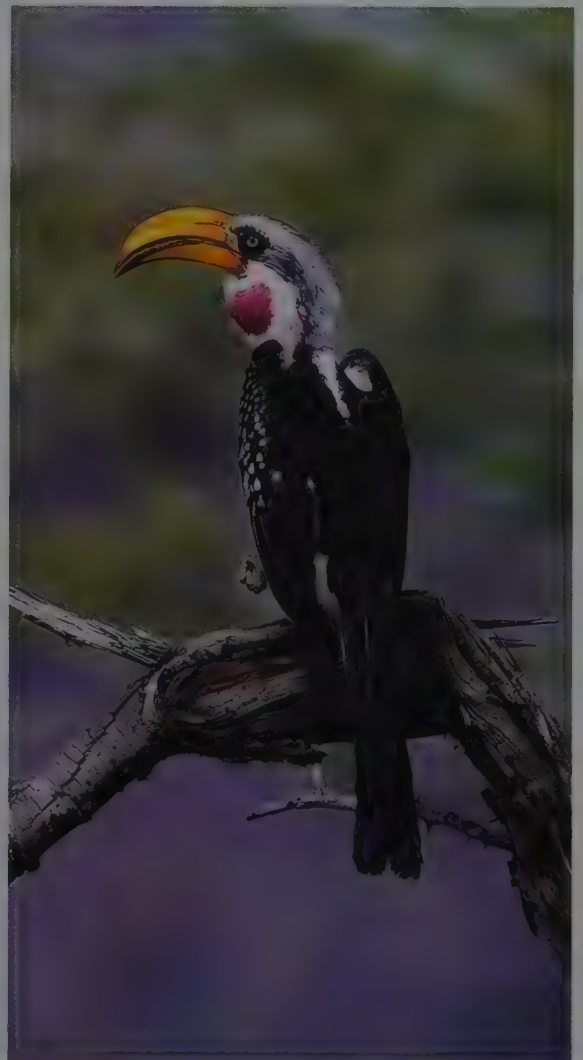
Some other species of hornbill gather in loose flocks, usually in small numbers, but occasionally in hundreds or even thousands. The smaller flocks often comprise either a few family groups that have come together, or an assemblage of non-breeding adult and subadult individuals that do not have territories or mates. These non-breeding groups seem to wander more widely than do adult pairs or groups, and they often pass through an area and then are not seen again for weeks. Larger groups are usually formed at food sources, such as fruiting trees, but generally they are made up of pairs or smaller groups which arrive at, and depart from, the food supply independently. Big groups sometimes collect also in drier savanna areas when periods of drought cause birds to move away from the driest areas and to form into flocks, which roam nomadically in search of food. This behaviour is known to occur with, for example, the Red-billed and Bradfield's Hornbills. In Thailand's Khao Yai National Park, all four hornbill species gather

in groups during the non-breeding season, with maximum recorded flock sizes of 54 for Austen's Brown Hornbill, around 70 for Great Hornbills, about 130 for Oriental Pied Hornbills (*Anthracoceros albirostris*) and up to 1000 for Wreathed Hornbills.

The largest assemblages of hornbills are observed at communal roost-sites. This applies especially to the larger forest species that feed mainly on fruit, such as some of the *Rhyticeros* hornbills in Asia and the *Bycanistes* hornbills in Africa. A well-publicized theory is that these gatherings may serve as centres of information for new arrivals: the latter, by following long-time residents as they leave a roost in the morning, can quickly locate fruiting trees within the general area during the course of that day. It is also probable that roost attendance confers some advantage on a hornbill in terms of lowering the likelihood of its suffering nocturnal predation. Small flocks can often be seen heading towards the roosts in the evening, often with a marked regularity of time and direction, and leaving again the next morning. Roosts often contain several hundred individuals, and for a few species, such as the Plain-pouched and Wreathed Hornbills, the number can exceed a thousand birds. Indeed, the Plain-pouched Hornbill has formed the largest aggregation ever recorded for any hornbill species, with 2421 counted travelling to roost in northern Malaysia. Historical accounts of this species reveal that huge numbers, possibly in excess of this figure, assembled at favoured roost-sites in the Sittang Valley and the northern Mergui Archipelago, in Myanmar. These massive gatherings of rainforest hornbills are wonderfully noisy and visually stunning, and must surely rate among the foremost spectacles of the bird world.

Until recently, the Eastern Yellow-billed Hornbill, inhabiting an area from Ethiopia to Uganda and Tanzania, was considered conspecific with its counterpart of southern Africa, the Southern Yellow-billed Hornbill (*Tockus leucomelas*), but reappraisal of the evidence has shown that two species are involved. While morphologically very similar, these two forms prove to have different calls and bare part coloration. In particular, the bare throat skin of the Eastern is bright pink, while that of the Southern is dusky flesh. These pouches are inflated with spectacular effect during the breeding season, so the difference in their colour is likely to be important. While clearly of common ancestral stock, these two taxa have apparently speciated because their ranges became separated by a belt of unsuitable habitat, in the form of miombo (*Brachystegia*) woodland, stretching across southern central Africa from coast to coast.

[*Tockus flavirostris*,  
Samburu National Park,  
Kenya.  
Photo: Dave Richards]







In general, frugivorous hornbills are arboreal forest-dwellers while carnivorous hornbills are semi-terrestrial savanna-dwellers. This pattern is something of an oversimplification, however, and conceals the fact that almost all hornbills are omnivorous, taking plant and animal food in different ratios. The long and slightly serrated bills of forest hornbills are useful implements when it comes to plucking ripe fruit from trees and to gouging sweet pulp from tough husks, as shown here by Indian Pied Hornbills in Sri Lanka and a Black Hornbill in Borneo. The long neck and bill of hornbills are well designed for gaining access to fruit that would otherwise be just out of reach, and the bill serrations help in gripping fruit efficiently and softening it before ingestion. In general, three main classes of fruit are consumed. The first are the figs that grow throughout the forests of Africa and Asia, providing a rich source of carbohydrate, water and calcium. The second are drupes or capsules, and these provide high quantities of lipids. And, last, are the juicy fruits with thick skins. The uptake of water from food is important to hornbills as they drink rarely, or never, and must ensure that they avoid dehydration. Figs are an important staple, especially in the breeding season, as they provide the necessary calcium for females to produce eggshells and for nestlings to grow bones, tissue and feathers. Almost all frugivorous hornbills have been recorded eating insects or small vertebrates, and the incidence of this tends to multiply greatly during breeding, presumably because of the calcium provided therein.

[Above:  
*Anthracoceros coronatus*,  
Sri Lanka.  
Photo: Patricio Robles Gil.

Below:  
*Anthracoceros malayanus*,  
Gunung Palung National  
Park, West Kalimantan,  
Borneo.  
Photo: Tim Laman]



In Africa, hornbills in the genus *Tockus* are largely insectivorous, but most will supplement their diet with a few small vertebrates and a variety of vegetable matter. Hemprich's Hornbill will take lizards and chameleons, as well as its staple insect diet, and it also forages on fruits of various types when available. Here it is snacking on the flowers and seeds of prickly-pear cactus (*Opuntia*), proving that it is very much an omnivorous generalist.

[*Tockus hemprichii*,  
Ethiopia.

Photo: Dick Forsman]



Individuals of most species of forest hornbill roost on a thin outer branch of a tree, often at a preferred perch that is used night after night. Such sites probably offer the best protection from climbing predators, which are presumably unable to reach the roosting bird without being noticed. Interestingly, whereas smaller hornbills often choose branches that are below the canopy, where they are also shielded from aerial predators, the larger species frequently perch in the open, or just in the lee of the canopy to protect them from the weather. Some of the small *Tockus* species on the African savanna roost close to a main branch, probably because this camouflages them among the more open trees and bushes. The fact that nocturnal predation is an issue is indicated by a young Great Hornbill in Thailand that fell to the ground at 04:00 hours, with injuries that matched the talon marks of a large owl.

Most hornbills return nightly to the same roost-site, or have a selection of regular sites within their territory amongst which they alternate at irregular intervals. Only a few species, either nomads that wander in search of fruit or ground-hornbills that traverse very extensive territories, do not have a regular roost-site; instead, they fly up into a tree or on to a cliff face at whatever place they happen to end the day.

During the course of the day, hornbills maintain themselves by means of a number of basic behaviour patterns as they go about their business. The major proportion of the time spent on maintenance activities is devoted to preening the feathers, and this activity, because of the long bill, frequently results in the adoption of awkward postures in order to reach the various parts of the body. The neck is often arched during preening of the breast, one wing at a time is held wide open to enable the bird to reach the primaries, or the tail is twisted and expanded to one side or the other. Allopreening is also a regular form of behaviour between pair-members, and especially between members of co-operative groups. It augments the care given by the individual in tending the plumage, even though its primary function is probably that of social facilitation. In addition, food is often passed back and forth between individual hornbills during such social encounters. Rather than being concerned with any nutritional requirement, this passing of food is probably more a test or expression of dominance, and such interactions over food are particularly common among members of co-operative groups.

Scratching with the foot is another aspect of behaviour that is also employed in order to arrange those feathers on the head

and neck that cannot be reached by the bill. The application to the plumage of preen oil from the gland at the base of the tail is an activity which hornbills carry out frequently. This is achieved either by nibbling at the gland with the tip of the bill, or by leaning backwards and rubbing the sides of the head across the gland. Special attention is paid to the bill and the casque, which involves rubbing them across a perch or a nearby branch, or biting repeatedly on a thin twig or piece of bark in order to clean the inside surfaces.

Hornbills often sunbathe, usually with the back facing the sun, the head feathers raised, the preen gland exposed, and the wings drooped at the sides to expose the back. Some species, however, adopt more elaborate postures. The *Buceros* hornbills, for example, perch with the wings open and the head lolling to one side, while others, such as the *Bucorvus* ground-hornbills or the African Grey Hornbill, even lie flat out on the ground with both wings spread.

Those hornbills living at higher altitudes, with colder temperatures, need to gain heat at the start of the day. Some of the smaller *Tockus* species show a type of "warming-up" behaviour in which they droop the wing on one side only, thus exposing the back to the morning sun. On the other hand, several species living in hotter climates have special postures designed to enable them to lose, rather than to gain, heat; either they spread the "wrists" to expose the bare skin under the wings, or they gape with the bill open so as to release heat from the lungs and the moist inner surface of the mouth. In the ground-hornbills, the upperwing-coverts are also raised to lose heat, producing a "chrysanthemum" effect. It is suspected that, in these and some other species, heat is also radiated via the extensive bare facial skin; some species inflate this bare skin, thereby increasing its surface area.

After rain, all bucerotid species dry out the plumage, holding the wings drooped and the tail fanned. Bathing in wet foliage is also performed after rain, either in wet grass on the ground or among the dripping branches above.

There are a few basic actions that are common to most of the Bucerotidae. When nervous, hornbills often make short, jerky movements of the head and neck, sometimes with the body held low and the head peering out from below the level of the perch. More aggressive behaviour involves lifting the bill to expose the colours of the throat and bare skin, and this often leads to re-directed aggression, shown by pecking hard at the perch; at times



In South-east Asia and Indonesia, fig (*Ficus*) trees are often the giants of the forest, and when in fruit they are one of the best places to watch hornbills, along with a variety of other creatures that visit to harvest the bounty. In this case the visitors to a Bornean fig tree are a male Wrinkled Hornbill and a female Wreathed Hornbill of the small Bornean form with reduced corrugation of the mandibles, formerly separated as race *aequabilis*. Elsewhere in Borneo it was shown that hornbills probably exploited less than a third of a total 900 fruiting tree species counted at a study site. As at this tree, it is common for several species of hornbill to converge on major food supplies; indeed, up to eight species can co-exist in the same forest, principally by partitioning resources. This occurs through different-sized species selecting different food sources and some preferring different vegetational strata. Because of their fruit-eating habits and their mobility, hornbills are vital vectors of seed dispersal and thus perform an extremely important function in the ecological balance of tropical forests.

[Above:  
*Aceros corrugatus*.  
Below:  
*Rhyticeros undulatus*.  
Gunung Palung National  
Park, West Kalimantan,  
Borneo.  
Photos: Tim Laman]



it can result in more serious conflict, including bill-wrestling or even real fighting. Special threat postures are adopted by only a few hornbill species, such as the White-crowned Hornbill, which spreads its wings and tail, or the Helmeted Hornbill, which crouches with the tail raised and the bill at the ready.

Certain types of behaviour also occur which have no obvious or immediate function. These include the mandibulating of sticks in the bill, the tossing over of debris, fast aerial chases, and contact actions such as bill-wrestling or jumping on or over each other. Such behaviour is seen most often from juveniles, especially in co-operative groups such as those of Southern Ground-hornbills (*Bucorvus leadbeateri*), and it is sometimes termed "play". Adult birds do sometimes perform these kinds of behaviour, but, as if disturbed by all the activity, they also interfere with groups of playing juveniles and break them up.

Only a few species of hornbill have a ritualized form of territorial display, and these are mainly the ones that feed more on animal foods and are territorial throughout the year. This applies to most of the small *Tockus* species of Africa, some of which perform displays with the head bowed and others executing this behaviour with the head raised, the display being elaborated further in some cases by the opening of the wings and the spreading of the tail. At least two, quite unrelated species end their display by fanning the tail above the back; these are Hemprich's Hornbill in Africa and the Rufous-necked Hornbill on the Asian mainland. Closely related species often perform very similar display movements. This is shown to be the case with the Eastern Yellow-billed and Southern Yellow-billed Hornbills and Von der Decken's Hornbill (*Tockus deckeni*), although the species differ from one another in details of the bill colours and plumage patterns and, therefore, in the signals which they convey. Loud vocalizations accompany these displays, and in most species loud calls alone are used as the principal form of advertisement, territorial proclamation and long-distance communication.

### Voice

The loud calls of most bucerotid species are among the most obvious of all animal sounds wherever these birds occur. The reason for this is that hornbills tend to be conspicuous birds, and

they need to make their presence known to one another. Calls are an especially useful means of communication in dense habitats, such as the forest that is occupied by so many hornbill species, but they are also an important adjunct to the visual signals and displays used by other hornbills in more open savanna habitats. Non-territorial species use their loud calls primarily to maintain contact, as when flocks fly to and from roosts, or when individuals gather at fruiting trees. Perched hornbills may call to attract the attention of flying birds, and flying ones may call to retain flock cohesion. Territorial species also use their loud vocalizations to make contact, but they employ them most frequently to proclaim possession of a defended area, especially during the breeding season. Some sedentary and territorial species, such as the ground-hornbills, utter their deep, booming calls almost every dawn, besides at intervals during the day whenever they encounter or suspect incursions into the territory.

Often, the two members of a territorial pair of hornbills will call in unison, and in several species the calls are given with special postures or active displays. These displays are developed to the greatest degree by the small *Tockus* hornbills of the African savanna. Here, the main distinctions are between species which call with the head bowed down and those which raise the bill skywards, and between those which fan the wings or tail and those with no special posture. Of particular interest is that all adult members of co-operative groups usually call together, and the vocalizations of each sex can often be distinguished by pitch, so that the sexual composition of a group can be ascertained by neighbouring hornbills, or by researchers, listening at a distance. The loud calls probably function also in mate attraction, as when a single bird attempts to bring a mate into its territory, or when neighbours hear that an individual of a particular sex is missing from a breeding group.

Loud calling can occur at any time of the day. It is usually most frequent in the early morning, but in the African savanna the calls of hornbills are also one of the few sounds heard during the heat of the day. Ground-hornbills, in particular, call regularly in the period before dawn, and it is thought that this may be to facilitate transmission of their deep, low-frequency sounds in the still air that is layered at different temperatures and densities.

Most hornbill species can be easily identified by their calls, although some closely related species have rather similar utter-

In the African savanna *Tockus* hornbills are known to consume many invertebrate taxa. The distribution of animal foods is usually less clumped than is that of fruit, and it is thus more universally available but more time-consuming to locate each item. As a result, predatory hornbills tend to be more sedentary and territorial than their frugivorous counterparts. This Southern Yellow-billed Hornbill, however, has been lucky enough to find a rich source of insect food: swarms of white butterflies (*Pieridae*) attracted to damp mineral-rich ground.

[*Tockus leucomelas*,  
Moremi National Park,  
Botswana.

Photo: Rafi Ben-Sahar/  
Oxford Scientific Films]







ances. Calls vary from simple single syllables to complex multi-frequency combinations. The larger species also tend to have deeper and louder calls than those of the small species. Ground-hornbills utter deep, booming notes that are audible at up to 5 km under the ideal conditions of the still pre-dawn period; these calls could be mistaken for the grunting sounds made by a lion. Small *Tockus* hornbills can be divided between "whistlers" and "cluckers", exceptions being the specialized forest species, namely the Black Dwarf-hornbill (*Tockus hartlaubi*), the Red-billed Dwarf-hornbill and the Long-tailed Hornbill, each of which has its own, very different, peeping, hooting or howling calls. The *Bycanistes* and *Ceratogymna* hornbills inhabiting the African forest make loud braying notes, usually rather raucous and nasal; these are given mainly by the male and are often drawn out into wailing baby-like calls, as typified by the Trumpeter Hornbill. In the Asian forest, the huge hornbills of the genus *Buceros* have loud roaring calls, often given by a pair in duet and reaching a crescendo as the two take flight. The Helmeted Hornbill differs with its unique call, an accelerating series of single hoots that breaks into loud cackling laughter, one of the loudest and most dramatic calls of any bird. Large *Aceros* and *Rhyticeros* hornbills, on the other hand, emit just a few simple barking notes, unlike the aberrant White-crowned Hornbill, which utters a series of pigeon-like cooing notes. The other, smaller Asian hornbills give mostly complex cackling calls, such sounds being made by, for example, the *Penelopides* tarictic hornbills and being reflected in the onomatopoeic name of those species. Once again, however, there is an exception, in this case the Black Hornbill, which has rasping, braying calls.

Apart from their noisy calls, hornbills also produce a variety of simpler and quieter vocalizations, which are usually similar in structure to the loud calls. Soft contact calls are often heard between members of a pair, or are used to maintain cohesion among members of co-operative groups. Sometimes, they serve to attract attention to potential prey, as when ground-hornbills surround a snake to prevent its escape. At other times, they indicate the presence of fruit, as instanced by the quiet chuckling sounds that reveal hornbills feeding at a productive tree. Chicks within the nest emit harsh begging calls when waiting for food, and they

utter an especially loud "acceptance screech" when they actually receive the food. A female often makes a similar screech when taking food presented by the male in courtship. Most hornbills also utter a short squawk of alarm when frightened by the sudden appearance of a predator.

Many of the larger hornbill species are audible in flight as a result of the whooshing sound of their deep wingbeats. This sound arises from air flowing through the bases of the flight-feathers, since these birds lack underwing-coverts, and whistling over the two small outer primaries, which are stiff and emarginated. It is often possible to determine the identity of a species from the sound of its wingbeats, which makes it likely that these sounds function also in communication. They could, for example, assist cohesion among members of a flock in flight, or alert perched birds to the movements of neighbours and to the passage of other groups. Hornbills can also make loud sounds by pecking at a perch, especially if it is a dead log, and this is a form of communication used in aggressive situations.

### Food and Feeding

Most hornbills are omnivorous, eating a combination of animal and vegetable foods, although there is a tendency for each species to eat mainly fruit or mainly small animals. Each species of hornbill has specific food preferences, foraging techniques and, within the forest, preferred foraging heights. As a result, up to eight species may co-exist within an area, each one having its own particular feeding niche. Most of the predominantly frugivorous species live in forest, while the majority of species with carnivorous tendencies live in savanna habitats.

The proportions of different types of food in the diet vary during the year, depending mainly on availability. There is, however, a tendency for frugivorous species to become more carnivorous, and to include more animal protein in their diet, when nesting. Most hornbills never drink water, and even for the few species for which it has been reported drinking does not appear to be regular or essential, with the possible exception of the larger *Ceratogymna* species. Water must, therefore, be obtained from

When searching for fruit in the canopy of trees, the Grey-cheeked Hornbill will consume whatever animal food it encounters. In this case it has plucked a large spider from its leafy lair, but it will also snap up millipedes, snails, lizards, bats, birds or small mammals such as galagos. Like several other forest-dwelling hornbills it often forages in groups and follows squirrels and troops of monkeys to glean the creatures that are flushed by the activities of the advancing mammals.

[*Bycanistes subcylindricus subquadratus*, Entebbe, Uganda. Photo: Joe McDonald/DRK]



Visiting its nest, this male African Grey Hornbill carries a large centipede (*Scolopendra*) to offer to its mate. Once the breeding cycle begins, the female remains within the nest cavity and the male provides food for both adults and, initially at least, for the brood after hatching. This is a busy job and male hornbills are so tuned to the task that they occasionally offer food at nests that are not their own, sometimes even containing different hornbill species. Even before nesting, males have been seen to offer food at the empty nest-hole before the female has begun to incubate.

[*Tockus nasutus epirhinus*, near Marondera, Zimbabwe. Photo: Peter Ginn/ARPS/APSSA]



Most terrestrial hornbills at least occasionally dig for food. This behaviour is most regular and conspicuous in the ground-hornbills: they occasionally become so engrossed in pursuing fossorial prey that they lie down to reach more deeply into the pit they are digging. Most hornbill excavations are minor affairs, however, and usually involve flipping over debris that might conceal food items or rummaging lightly in soil. The Red-billed Hornbill often digs in dung for small invertebrates, which is presumably the purpose of this individual, although it is likely that dung is sometimes collected and used to plaster the nest entrance.

[*Tockus erythrorhynchus erythrorhynchus*, Samburu Game Reserve, Kenya.  
Photo: Joe McDonald/Animals Animals]



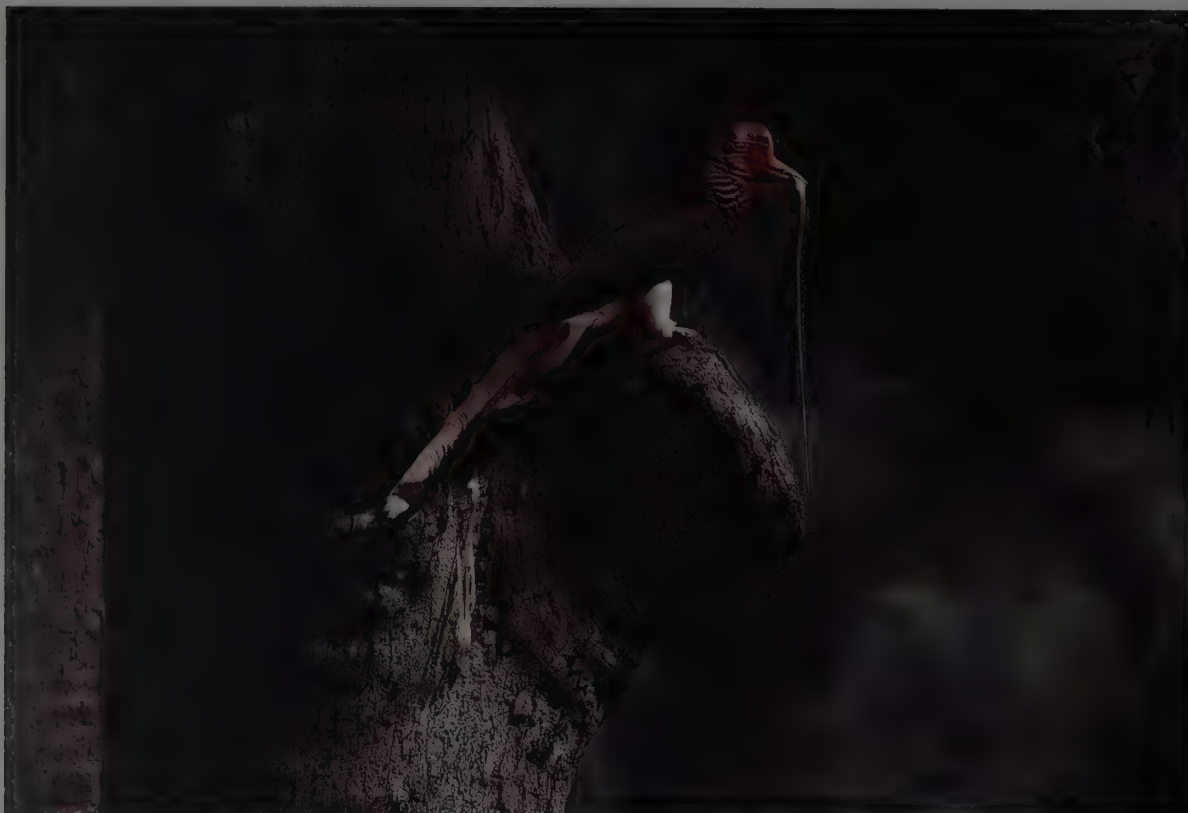
the food, so that some food may be selected more for its liquid than for its nutritional content, and the special kidney structure of the Bucerotidae (see Systematics) may also be important in maintaining water balance. The two ground-hornbills sometimes dribble liquid from their nostrils after feeding, suggesting that they possess as yet undescribed salt glands to excrete the excess salts from their carnivorous diet.

Hornbills occupy a variety of ecosystems, situated within several different floral and zoological assemblages. This brings each species into contact with a different set of plants and animals, among which it must survive and find food. Ripe fruits of three main categories are selected. These are figs, which are rich in carbohydrates, water and especially calcium, drupes or capsules, which are rich in lipids, and other juicy fruits, housed in thick husks. Figs often form the dietary staple, even when adults are forming eggs or raising growing chicks, this being due to their high calcium levels. Other fruits are taken as available, or when needed to provide fats for chick-raising or to supply liquids to counter possible dehydration. In Africa, Grey-cheeked Hornbills in Uganda ate fruits of 67 plant species of 42 genera, while in Gabon there were about 120 species of fruiting plant that could supply food for the members of this family. Several Asian hornbill species have also been recorded eating fruits of at least 30-35 different plant species during the breeding season alone. Even so, the fruits eaten form only a subset of those available. In Kalimantan, Borneo, hornbills were found to consume fruits from 128 tree species, and probably to exploit a further 144 species, but altogether there were over 900 species of fruit present in the study area.

The various items of animal prey taken by hornbills cover most major vertebrate and invertebrate orders, and at least 100 taxa may be taken by small *Tockus* hornbills living on the African savanna. Ground-hornbills, the most carnivorous of all bucerotids, capture prey as large as hares, cobras, squirrels, mongooses and tortoises. The principal constituents of their diet, however, are arthropods, especially insects and arachnids, and these also form the main animal prey of most other carnivorous hornbills. In addition, myriapods, molluscs and crustaceans are regularly taken as food items when available. Ground-hornbills

forage by walking, covering a distance of up to 11 km in a day, and consuming any animal encountered which they can overpower, sometimes after a short terrestrial or aerial pursuit. They attend grassland fires that flush out concealed prey, and they associate with herds of ungulates that perform the same service by the action of their hooves. Ground-hornbills often dig for prey, particularly in the dry season, and especially in the vicinity of elephant dung or into wasp or bee nests, from which they extract combs and honey. On rare occasions, ground-hornbills attend carcasses or lion kills, although their main objective may be the collection of insect larvae rather than the carrion itself. They have been recorded eating small pieces of bark and sticks, but in general they rarely consume vegetable matter. Undigestible remains are regurgitated as loose pellets.

Most Asian forest hornbills were once thought to be exclusively or largely frugivorous. More recent research, in particular involving nest watches of certain species, has revealed a surprising variety of food sources targeted by breeding hornbills. The diet of nestling Rufous-necked Hornbills studied by V. Chimchome and co-workers at Huai Kha Khaeng, in Thailand, for example, consisted of 13 identified types of fruit and at least 20 types of animal. The fruit belonged to the floral groups Lauraceae, Moraceae, Myrsinaceae, Meliaceae, Flacourtiaceae, Myrtaceae, Anacardiaceae, Annonaceae and Burseraceae, while the animal food included beetles, butterflies, caterpillars, cicadas, click beetles (Elateridae), orthopterans, centipedes, crabs, millipedes, scorpions, both non-flying and flying lizards, geckos, skinks, earthworms, fish, frogs, birds and eggs. Nest watches of four hornbill species at Khao Yai National Park, also in Thailand, have recorded a variety of mammals, such as bats, squirrels and rodents, reptiles, including the green pit viper (*Trimeresurus stejnegeri*), and birds, these last including barbets, nightjars (Caprimulgidae), bulbuls (Pycnonotidae), pigeons (Columbidae), Collared Scops-owls (*Otus bakkamoena*) and a Greater Racquet-tailed Drongo (*Dicrurus paradiseus*). They also provided snails, crabs, worms, frogs and fish. Far from being obligate frugivores, therefore, the hornbills of the South-east Asian forests prove to be formidable predators of animal prey. The astonishing spectrum of foodstuffs which they deliver at the nest is obviously



This Helmeted Hornbill aptly demonstrates the propensity of frugivores to seek vertebrate (in this case reptilian) prey in the breeding season. Although this species has a diet made up mostly of fruit, it regularly dedicates about half of its day to the business of foraging for small animals, typically in the canopy of the forest's tall trees. Within their home range, the members of a pair tend to hunt separately. As well as snakes, they will take squirrels and birds, and sometimes even feed on smaller hornbill species. The casque of this species is unusual in design: it is the only completely solid casque structure in the family.

[*Rhinoplax vigil*,  
Klong Saeng Wildlife  
Sanctuary, Thailand.  
Photo: Adisak Vidhidharm/  
Thailand Hornbill Project]

collected not only in the canopy, but also from the understorey and the forest floor, and seemingly from around streams and pools as well. It appears that hornbills increase their use of animal foods during the nesting season, particularly after the chicks have hatched, presumably in order to meet the calcium requirements of egg production and nestling growth. At other times of year, they revert to a more frugivorous diet.

Several hornbill species associate with other animals while hunting. Those *Tockus* species that live in forest habitats will follow army ants, parties of other bird species, bands of squirrels or troops of monkeys for the insects they disturb. On the African savanna, Eastern Yellow-billed and Von der Decken's Hornbills follow bands of dwarf mongooses (*Helogale undulata*) and capture the locusts disturbed by those mammals. This behaviour has even developed into a mutual relationship, in which the hornbills take over sentry duties to warn mongooses of the proximity of predators shared by both parties, and in which each participant has a special type of behaviour to stimulate the other to co-operate. Observations made by A. Rasa in Kenya revealed that, each morning, the hornbills waited outside the termite mounds in which the mongooses slept, even waking up the mammals if they did not rise early enough; the mongooses, for their part, would not set out to forage until the hornbills had joined them. Interestingly, when drought conditions caused the hornbills to switch their attentions to foraging alone in trees, the hunting behaviour of the mongooses was less efficient, as they had to spend more time on guard duties. Other carnivorous birds will also sometimes accompany hornbills, examples being the *Melierax* chanting-goshawks that follow ground-hornbills in Africa and the *Spizaetus* hawk-eagles that associate with Asian forest hornbills.

Animal foods are usually relatively evenly distributed across the habitat, but are difficult to find. Most carnivorous species are therefore sedentary, territorial and rather thinly spread across their chosen habitats. Territory size varies from as much as 100 km<sup>2</sup> for the ground-hornbills down to 1-2 km<sup>2</sup> for the huge Asian hornbills, and to as little as 10 ha for the small African terrestrial *Tockus* hornbills. This allows individuals or groups of each species to defend an area in which they can hunt undisturbed, spend relatively long periods searching for food, and learn the daily and seasonal details of where and when to find prey.

Fruiting trees, on the other hand, tend to have a patchy distribution and to be clumped in both space and time. In order to cope with this unpredictability, the frugivorous hornbills develop special types of behaviour to enable them to locate and track their food sources. Most species are not territorial, since they have to range widely in search of fruiting trees, and they are not evenly distributed, since they tend to congregate in flocks and around fruiting trees. Some large Asian forest hornbills are estimated to range over about 300 km<sup>2</sup>, and the largest African frugivorous species have been tracked to at least 100 km from where they were originally captured. The majority of frugivorous hornbills also have good communication abilities, allowing individuals to keep in contact while they search for food. Most gather at communal roosts, which may serve as centres of information (see General Habits), have loud flight calls and wingbeats to enable them to maintain contact (see Voice), and keep together in loose flocks (see General Habits). Furthermore, several different species may congregate at sources of food, or assemble to share communal roost-sites.

Medium-sized to large hornbills can consume 100-300 ml of fruit in one session, an amount which can be made up by anything from four large figs to 200 small ones. Seeds from these and other fruits are regurgitated within an average time of 67 minutes, the period ranging from 19 to 110 minutes, or they are expelled by defecation after a slightly longer average time of 83 minutes. The selection by these birds of fresh fruit, free of insects, coupled with the fact that the seed does not suffer any damage during its passage through the digestive tract, makes the Bucerotidae well suited to disperse the seeds of forest plants. The mobility of hornbills, with average ranging velocities of 200-1200 m per hour, also contributes to their efficiency as agents for seed dispersal (see also Status and Conservation).

Hornbills use the bill to collect food, employing a variety of techniques. The simplest method is just to pick up food where it is found, and this is, of course, the main technique applied when taking fruits. A hornbill will uncover concealed food by levering over or lifting objects, or by digging into the ground, under bark or into soft wood. Not surprisingly, digging is most prevalent among the terrestrial species, and in the case of the Southern Ground-hornbill this behaviour may culminate in the bird lying





Hornbills often manipulate and carry food items in the tips of their mandibles.

These Great Hornbill photos illustrate such behaviour with a small fruit (above) and a bird's egg (below). This species is an observant and opportunistic predator that will exploit almost any resource according to availability. It is not clear to what extent animal food is directly sought or accidentally encountered. Certainly, if nests of other species are found, the contents soon become a meal. Hornbills in Khao Yai National Park have been recorded taking eggs from open nests, including those of bulbuls (*Pycnonotidae*) and doves (*Columbidae*), although accurate egg identification during nest watches is extremely difficult.

[*Buceros bicornis*,  
Khao Yai National  
Park, Thailand.  
Photos: Atsuo Tsuji/  
Thailand Hornbill Project]



The diet of the Red-billed Hornbill generally consists of small adult and larval insects such as beetles, termites and grasshoppers. It will, however, seek and consume small vertebrates such as geckos and rodents. The long neck and bill of hornbills provides access to another vertebrate food source: passerine nestlings. In this case an individual has found an easy meal at the nest of a White-browed Sparrow-weaver (*Plocepasser mahali*).

[*Tockus erythrorhynchus erythrorhynchus*, Kenya.  
Photo: A. Wharton/FLPA]

down to dig as deeply as it can reach. Hornbills will snatch hanging fruit or active animal prey from vegetation or the ground while in flight, and they will even hawk aerial prey on the wing. Most items are simply swallowed whole. Large items, however, may be broken up, separated into edible and inedible parts, as by removing fruit husks or insect wings, and then crushed or softened in the bill. Certain distasteful foods, such as sticky fruits or hairy caterpillars, or slimy items, may be wiped on a branch or the ground before being swallowed.

On the bucerotid bill, the tips of the mandibles always meet precisely, as with a good-quality pair of forceps. They can be used delicately, so as to procure a bird's egg without breaking it, or with force, in order to crush a skull or break open a fruit capsule. Only in a few small *Tockus* species, however, do the inner surfaces of the mandibles meet, forming sharp cutting edges. In most other hornbill species, they are separated by a gap, as with a pair of nut-crackers, and in many such species the inner cutting edges are serrated, forming a strong instrument for cutting, crushing and softening the food. The long, flexible neck provides strong support to the skull and bill, especially in those species, such as the ground-hornbills, that dig for food. The neck, together with the long bill, also provides a useful extension for reaching fruit or for capturing fleeing or dangerous animals. The ability to reach far out to pick fruit, aided by support from the stout strong legs and broad grasping feet, and the wide gape, especially in larger forest species, are eco-morphological features which the Bucerotidae share with the New World toucans. Compared with the toucans, however, hornbills have only a short tongue, and so they pick up food in the bill tip and then toss it backwards into the throat to swallow, always with great control and agility.

## Breeding

The nesting habits of hornbills have long attracted attention, ever since it became known that the female of most species seals herself into a nest-cavity and leaves only a narrow slit through which the male passes her food. Even more interestingly, the female hornbill, while incarcerated, often becomes flightless through a simultaneous moult of her main flight-feathers and tail feathers. Furthermore, she and the chicks keep the nest clean by squirting

their droppings out through the slit in the sealed nest entrance. Only the two species of ground-hornbill do not seal the nest entrance or show any special moult, nor do they exhibit any particular behaviour with regard to nest sanitation. The basis of the curious nesting behaviour of hornbills probably lies in the anti-predator advantage that it confers upon the occupiers of sealed cavities. It has been shown that hole-nesting birds suffer lower predation rates than do those that build open nests. Furthermore, arboreal mammals, such as the yellow-throated martin (*Martes flavigula*) and the binturong (*Arctictis binturong*) in Thailand, sometimes prey on nesting female hornbills and their eggs or chicks. This predation pressure is presumably reduced by minimizing the size of the entrance slit.

The complete dependence of the female on the male throughout the nesting cycle also means that hornbills, with the possible exception of some co-operative breeders, always nest as monogamous pairs. Among the non-territorial forest species, pair formation often seems to occur some time before maturity, possibly in the roaming flocks of juvenile and non-breeding birds that are reported for most species. In the more sedentary species, the pair-members usually remain together throughout the year, so that mate attraction is not normally observed. In co-operative species, the dominant, or alpha, breeding pair is assisted by other members of the group, usually adult males, in such matters as the defence of the territory, the supply of lining material for the nest and the delivery of food, some additional help in the last two roles being provided by any immature birds present in the group. That some of these adult male helpers sometimes also attempt to copulate with the breeding female is indicated by the way in which the alpha male carefully guards the female. In a few monogamous pairs of hornbills, a second male has occasionally been observed to assist at the nest. In others, however, extra adults that visit the nest have more aggressive intentions, and sometimes disrupt the breeding attempt or capture the nest-hole.

As already mentioned (see General Habits), co-operative breeding is known to occur in eight species, and is suspected to occur in a further ten. While up to a third of hornbill species might therefore adopt a co-operative mating system, its origins or function in this family have not been exhaustively studied and explanations for such behaviour are, in any case, difficult





The most carnivorous of all hornbills are the Bucorvinae, like these Southern Ground-hornbills. They have been recorded capturing and consuming prey as large as hares, cobras, squirrels, mongooses and tortoises. Their diet mainly comprises arthropods, however, which they hunt by slowly walking through the grassland. On detection, the food item is picked up swiftly, sometimes after a brief chase, and tossed into the air to manoeuvre it before swallowing.

When provisioning females and offspring, males of some hornbill species will ingest several items and regurgitate them at the nest, while others carry a single item in the bill. In general, one of these two options is adopted, but the ground-hornbills are unusual in that they collect several items without swallowing them, and carry them lined up one after the other in the bill. The only other species that seems to do this is Monteiro's Hornbill (*Tockus monteiri*).

[*Bucorvus leadbeateri*, Masai Mara, Kenya. Photos: Günter Ziesler (above); Joe McDonald/DRK (below)]

to test. It is certain that group-living assures reproductive benefits to the dominant pair, as helpers provide extra food for nestlings or fledglings, as well as increased vigilance and defence against predators. What is less clear is how the helpers themselves benefit from the arrangement. The most promising adaptive explanations for co-operation in raising young involve kin selection or demographic constraints. According to the first of

these ideas, co-operation is worthwhile because it enhances the reproductive success or the survival of relatives. For example, if young Bushy-crested Hornbills are unable to find a mate or territory because all females are paired and the habitat is saturated, it may benefit them to assist their parents in raising another brood, as the offspring will contain many of their genes. The second notion relies on costs of dispersal, such as predation or the failure to secure a mate or territory. Young males that remain on the natal territory might therefore postpone these dispersal costs and accrue certain benefits, namely the possibility of opportunistic matings with the dominant female and an improved likelihood of exploiting future pairing opportunities in or around the natal territory. It is likely that the evolution of co-operative breeding by hornbills involves a combination of these factors, but clarification of the issue will take many years of intensive fieldwork and genetic analysis of study populations.

All species of hornbill nest in natural cavities. These are usually in trees, but sometimes in rock faces where they are available. The only variation on these preferences is that a few species use the old nest-hole of a large barbet or woodpecker, while the ground-hornbills will, on rare occasions, nest in the disused open stick nest of another bird species or will excavate a cavity in an earthen bank. An increasing number of hornbill species will use an artificial cavity if that is provided, such sites ranging from the bee-hive logs adopted by ground-hornbills in Nigeria to the modified nesting logs supplied in the rainforest of Thailand. In the arid semi-desert of Namibia, where there are few trees, the members of a large study population of Monteiro's, Red-billed, Southern Yellow-billed and African Grey Hornbills now breed in man-made nestboxes. The final selection of the cavity appears to be made mainly by the female. She is often assisted by her mate, which delivers food, lining material and, in some species, sealing materials to her while she is trying out the cavity, before sealing herself in.

Many nest-sites are used in successive seasons, and often the same pair of adults is involved. In addition, competition for nest-sites sometimes exists, both within and between species, so that a favourite site may be used by two or three species in succession or, among smaller species, one tree may contain enough cavities to house two different species simultaneously.



Ground-hornbills often consume reptiles, including venomous snakes. This Southern Ground-hornbill is in the process of swallowing a Puff Adder (*Bitis arietans*), a common snake that is responsible for the majority of human snake-bite fatalities in South Africa, at least. The bird relies on the rapidity of its attack and the length of its bill to ensure that it will not suffer adversely from the snake's defensive strike. Snakes are often fairly difficult to catch and can move quickly and inconspicuously through tall grasslands. When a snake is encountered, ground-hornbills sometimes forage co-operatively, with all group members surrounding the reptile so that it can not escape. Small mammals, too, appear on the diet of the ground-hornbills with relative frequency. Once captured, all such larger prey items tend to be crushed in the bill to overcome any initial resistance, and subsequently to make the prey easier to swallow and digest.



[*Bucorvus leadbeateri*, Kruger National Park, South Africa.  
Photos: Nigel J. Dennis/  
NHPA (above);  
Tim Laman (below)]



The Southern Ground-hornbill will occasionally help itself to a meal of carrion if the opportunity presents itself. Here a family group is picking at the carcass of a zebra (*Equus burchelli*).

While chunks of meat are certainly devoured, it is likely that the hornbills are also attracted to the rich supply of adult and larval insects that quickly colonize corpses on the savanna. Note the juvenile bird, with its browner plumage and duller, yellowish facial skin.

[*Bucorvus leadbeateri*,  
Masai Mara, Kenya.  
Photo: M. & C. Dennis-  
Huot/Bios]



The pair often visits several holes before choosing the final site, although the numerous cavities that are used repeatedly over many years do not require annual selection. The pair also becomes especially territorial prior to nesting, and this applies even to frugivorous species that are not normally territorial, but which, at this stage in the cycle, defend at least the area around the nest. Species that exhibit year-round territoriality often become vigorous in their defence of the nesting area; a group of five Southern Ground-hornbills, for example, has been recorded swooping on and killing an adult Verreaux's Eagle (*Aquila verreauxii*) that passed close to their nest at dusk. In several species, the colours of the facial skin become especially bright before breeding, while any displays that occur are performed more intensely and repeatedly, and often the male remains in close attendance upon the female in order to guard his paternity. The male will frequently offer the female food in courtship feeding, but sometimes he will also offer food at the cavity entrance, even when the female is nearby and perched outside the nest; this suggests a strong attraction to the nest itself. The female, prior to sealing in, may spend long periods sitting quietly in the nest, pecking at the walls, rearranging lining or accepting food. Such pre-nesting behaviour can sometimes extend over several months, at variable intensity, when conditions for breeding remain unsuitable through lack of rain or because of some other limiting factor.

Most hornbill species are seasonal breeders, especially in those habitats where there is a marked wet or monsoon season separated by a drier period. Species of the African savanna and woodland all start to breed at the onset of the rains, when mud for sealing becomes available, but more especially because arthropod food increases in abundance and accessibility at that time. Many savanna trees come into leaf in anticipation of the rains, and it is notable that arboreal-foraging species, such as the African Grey Hornbill, start to lay eggs before their ground-foraging counterparts such as the Red-billed and the Southern Yellow-billed Hornbills do. In at least the Southern Ground-hornbill, early egg-laying is correlated with a higher probability of successful breeding.

Many frugivorous hornbills lay only when fruit is sufficiently abundant either to support the female for egg-laying or to nourish the chicks after their emergence from the nest. The latter strat-

egy is suggested by the breeding timetable of several hornbill species of different sizes in Thailand: each has a nesting cycle of different duration, but all start in the height of the dry season, with hatching or fledging nevertheless synchronized to coincide with the onset of the drenching monsoon rains. In less seasonal tropical rainforest, nesting may occur at irregular intervals, and often not annually, since bouts of fruiting might be triggered at any time by a period of low, rather than high, rainfall. In such regions, the timing of nesting by hornbills may appear aseasonal, even though regular or synchronized breeding cycles are often followed by individual pairs or in particular regions.

Once conditions suitable for breeding develop, copulation occurs at intervals during the day, either around the nest, during visits for its preparation, or away from the nest. Various types of pre-copulatory behaviour have been described. These range from strenuous allopreening of the female by the male until she crouches for copulation, as in the ground-hornbills, to repeated jumping back and forth over the female by the male, as in some large *Bycanistes* and *Buceros* species. Preliminary sealing at the nest also starts at about this time, the female either closing up cracks and grooves on the outside or partly closing the entrance from within. By preference, most hornbills choose as small a nest entrance as possible and, where available, one that already resembles a vertical slit, since this reduces the amount of effort and material needed for sealing. In most species, the female uses mud collected near the nest if she is working from the outside, but, once within, she uses her own droppings or food remains. Generally, the male does not assist, but in a few small *Tockus* hornbills the male sometimes brings lumps of mud in his bill tip, while in *Bycanistes* and *Ceratogymna* hornbills the male even swallows soil, which is then formed into sticky pellets in his gullet and regurgitated to the female.

As soon as the female has attained breeding condition, she seals herself into the nest. Contrary to many popular chauvinistic accounts of hornbill nesting, the male has no means of forcing the female to enter or of preventing her exit. The nest entrance is normally sealed to form an elongated vertical slit, which may be important in the regulation of separate airflows through the nest. Air is driven through the nest by the heat that has been generated by the warm-blooded occupants, sitting on the nest floor below



After choosing a nest-site, female hornbills begin to spend a high proportion of their time in and around the nest. During this phase of the breeding cycle courtship feeding rates increase. By offering prey to their mates, male hornbills might be augmenting the female's diet to maximize clutch size and egg quality, or they might be signalling their quality as a provider of resources. In addition to food items, males or group-members will often make contributions of lining or sealing materials to breeding females, as illustrated by this Red-billed Hornbill offering a leaf to his mate.

[*Tockus erythrorhynchus rufirostris*, Kruger National Park, South Africa. Photo: HPH Photography/Photo Access]

the level of the entrance, and it is replaced by cool air that flows in over the lip of the entrance.

Sealing of the entrance hole can be completed within a few hours, taking at most a few days. The female then sits in the nest for a pre-laying period of about four to six days, this only rarely extending to just over three weeks. Thereafter, the eggs are laid at intervals that range from one day, in the case of small species, to about five days, for large species. There is some variation in this basic pattern, often with an increase in inter-egg interval as laying proceeds, so that, for virtually all species, complete clutches can take up to 20 days to be laid. Hornbills are remarkable for the long time that elapses between the final copulation, just before the female seals herself into the nest, and the laying of eggs which are still fertile. With many other bird species, the viability of the sperm, and hence the chances of fertile eggs, decrease steeply within a few days of the last copulation. Among the hornbills, fertility remains high for at least three weeks. It seems that this is made possible by glands present in the female's oviduct that nourish the stored sperm, and, apparently, because sperm supply to the ovary is not overly disrupted by the passage of successive eggs down the oviduct.

Clutch sizes range from just one or two eggs, as with the large species, to as many as eight for some small *Tockus* species. The eggs of all hornbill species are white, with a pitted shell and, usually, a rather elongate oval shape. They vary greatly in size: those of the Red-billed Hornbill, about  $34 \times 24$  mm, represent one of the smallest, whereas the eggs of the Southern Ground-hornbill, at  $74 \times 52$  mm, are the largest.

For the majority of those species of Bucerotidae that have been observed inside the nest, it has been shown that the female starts to shed her tail feathers, or rectrices, after the first egg is laid, followed by the flight-feathers, or remiges, during the ensuing few days. The female either throws the moulted feathers out of the nest entrance, as she does with food remains and other debris, or sticks the feathers away in crevices within the nest. Within the confines of the sealed cavity, she has no choice but to start incubation from the time when the first egg is laid. Incubation takes from 23 days to 42 days, depending mainly on the size of the hornbill species in question. Since the chicks hatch in approximately the same order as that in which the eggs were laid, and at more or less the same intervals, the effect is to produce a

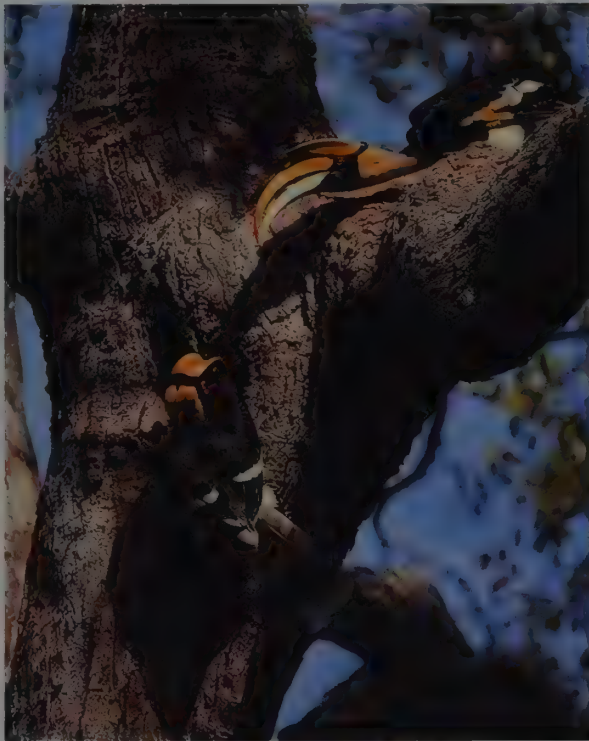
brood with the chicks staggered in size. This allows the largest nestlings to be more successful in competition for food and space, with the consequence that smaller chicks often die of starvation. The positive biological effect of this attrition is that the brood size is quickly and economically tailored to match the available food supply. Even if younger siblings only very seldom reach maturity, the benefits are sufficient to maintain production of surplus eggs over many generations.

The male brings food to the nest throughout the nesting cycle. Among co-operative breeders, he is assisted in this task by most members of the group. Provisioning rules vary among species. For example, dominant female Austen's Brown Hornbills in Thailand will apparently not allow subordinate females to feed the brood, while in Bushy-crested Hornbills all individuals sometimes assist at the nest. The female and, later, the chicks spend long periods waiting with one eye looking out through the narrow entrance, in anticipation of food being delivered. Food is sometimes transported to the nest in the bill, carried either as single items, as with most small *Tockus* hornbills, or as several items together, as is the case with ground-hornbills and some Monteiro's Hornbills, but most other hornbill species transport food as multiple items in the gullet. With the latter method, the multiple items are regurgitated one at a time from the gullet back to the tip of the bill, and are then passed singly into the nest. On occasions, however, an extra item, such as a juicy animal, is kept in the bill tip and presented before the main load of fruits. For obvious practical reasons, those species which eat smooth rounded fruits feed the young mainly by regurgitation, while animal-eaters usually carry their awkwardly shaped food in the bill.

Female hornbills are often reported by hunters and collectors to be noticeably fat on entering the nest and during incubation. This has been studied in detail only for Monteiro's Hornbill, the female of which was found to be fattest during incubation and then lost weight after the eggs hatched, possibly as a result of her passing food preferentially to the chicks. Nesting females, however, are far from passive and, indeed, have an active metabolism. This is necessary when the nest temperature drops below or rises above the thermo-neutral range of about  $17-30^{\circ}\text{C}$ .

The duration of the nestling period varies according to the size of the species. There is also individual variation in growth and feeding rates, so that the time spent by the young in the nest





This sequence of photographs reveals an interesting feature of the courtship process in some hornbill species. The male Great Hornbill appears to accompany his prospective female to a nest cavity and seems to persuade her to inspect it. While she enters, purportedly to assess its quality, the male awaits her judgement with interest. Given a favourable response, the pair sometimes copulates immediately after nest inspection.

The importance of selecting a cavity that meets the demands of space, safety and microclimate during the incubation and nestling periods results in a very thorough survey of potential nest-holes within the pair's territory. It is probable, however, that the male does not attract the female to the hole, as in many hornbill species she undertakes nest selection almost on her own and the link between nest approval and copulation has yet to be proven.

[*Buceros bicornis*,  
Khao Yai National Park,  
Thailand.  
Photos: Atsuo Tsuji/  
Thailand Hornbill Project]





the nest. In all other species, the female emerges more or less simultaneously with the chicks at the end of the nesting cycle; in the case of the large Wreathed Hornbill, this means that she has remained in the nest for up to 137 days, or more than four months.

The newly hatched chick is altricial, with pink skin and closed eyes. The upper mandible, with a white egg tooth at its tip, is markedly shorter than the lower one, giving a pugnacious appearance to the chick. Within a day of hatching, an air-sac develops under the skin of the shoulders and, within a few days, this spreads to cover most of the dorsal body surface, and even extends below, to the sides of the breast and under the wings. The young chick begs weakly for food with soft cheeping calls, and is fed directly by the female with whole food items, be they fruit or animal. In some genera of larger species, including *Bucorvus*, *Aceros*, *Rhyticeros* and *Bycanistes*, the colour of the chick's skin changes from pink to blackish within about a week.

When the chick is about ten days old, the eyes start to open and the feather quills begin to emerge from beneath the skin. The quills continue to grow out from the skin, but they do not immediately open, so that, when the chick is about one-third grown, it has a prickly appearance. This is often referred to as the "porcupine" or "pin-cushion" stage. Soon thereafter, the quills break open and the feathering then quickly covers the body, only the larger flight-feathers and tail feathers still having much further growth to achieve. By about the same time as the feathering emerges from the quills, the legs have attained almost full size, having grown much faster than the wings. This enables the chick to sit up well, to move easily around the nest, to take its own food at the entrance, and to squirt out its droppings. In some species, it is at about this stage that the female breaks out of the nest and leaves the oldest chicks to reseal the entrance themselves, which they do by using their droppings and any food remains. Chicks of either sex carry out the task of resealing the nest entrance, although in later life males will never again enter a nest-cavity. At the end of the nesting cycle, as the chicks themselves fledge in sequence with their age and development, the younger ones also reseal the nest if they are not ready to emerge with their older siblings.

When the female or chicks decide to leave the nest, the sealing material is pecked away from within, using the bill. This process usually takes only a few hours, and sufficient material is removed just to enable the bird to emerge. Emergence is generally achieved in the same manner as when initially entering the nest: the hornbill pushes out first the head, then one wing ahead

ranges from 39-50 days for the smaller species to 72-96 days for the larger ones. In some species, such as the ground-hornbills, the small *Tockus* hornbills and the three *Buceros* hornbills, the female usually emerges from the nest when the chicks are about one-third to a half grown; depending on the size of the species, this is about 42-112 days after she initially sealed herself inside

The most famous and remarkable feature of the breeding biology of hornbills is the voluntary incarceration of females during the course of the incubation and fledging periods, as seen here with a Wrinkled Hornbill. This tactic is unique amongst birds and involves the plastering of nest-holes with a mixture of droppings, mud and sticky food remains until only a narrow slit admits the passage of food from the visiting male. This behaviour sheds some light on bill morphology, as it becomes clear that the laterally compressed design with added casque is useful in two major ways: first, it provides a trowel shape, vital for performing the plastering job in the first place; second, a narrow bill allows for a narrow slit, and this is presumably important in ensuring that predators and competitors are successfully excluded.

[*Aceros corrugatus*, South-east Asia. Photo: Thierry Petit/Bios]



Female hornbills, because they are sealed into the nest, are entirely dependent on outside help for their food. This circumstance necessitates a high degree of paternal care, a vital duty that in some species is shared between members of a co-operative group. Different techniques are employed for transportation of different food types. Animal items are usually delivered singly as they are difficult to store and regurgitate, while smooth fruits are often crammed into the gullet and then delivered singly at the nest. This is only a general rule, however, as this Knobbed Hornbill attests.

[*Aceros cassidix*, Tangkoko DuaSudara Nature Reserve, Sulawesi. Photo: Tim Laman]



All hornbills nest in natural cavities, usually in trees but sometimes in rock faces or in the ground.

The smaller species often use holes excavated by other birds, such as woodpeckers (Picidae) or barbets (Capitonidae). Nest-holes can be used traditionally, often by the same pair of hornbills for many years in succession. Frugivorous species, such as the Rhinoceros Hornbill, become increasingly territorial as the breeding season approaches, and usually defend at least a small area in the vicinity of the nest-hole. The sealing behaviour of hornbills presumably stems from predation pressure and competition for nest-sites.

For example, eggs, nestlings and incubating female hornbills are regularly predated in Thailand by mammals such as the Yellow-throated Marten (*Martes flavigula*) and Binturong (*Arctictis binturong*). In addition, many cases are known of hornbill competitors, conspecific or otherwise, usurping occupied nests. Both cases suggest that pressure to secure the nest-hole from invasive species is intense, and this has presumably driven the evolution of the female hornbill's curious habit. In the nest, she moults all her wing and tail feathers almost simultaneously. If something happens to her mate or group that prevents them from feeding her, she will die, as, even if she breaks out of the nest, she is incapable of flight. Most females emerge from the cavity only when their flight-feathers are virtually regrown, from midway through the nestling period to the end.

[*Buceros rhinoceros rhinoceros*,  
Hala-Bala Wildlife  
Sanctuary, Thailand.  
Photo: Morten Strange]





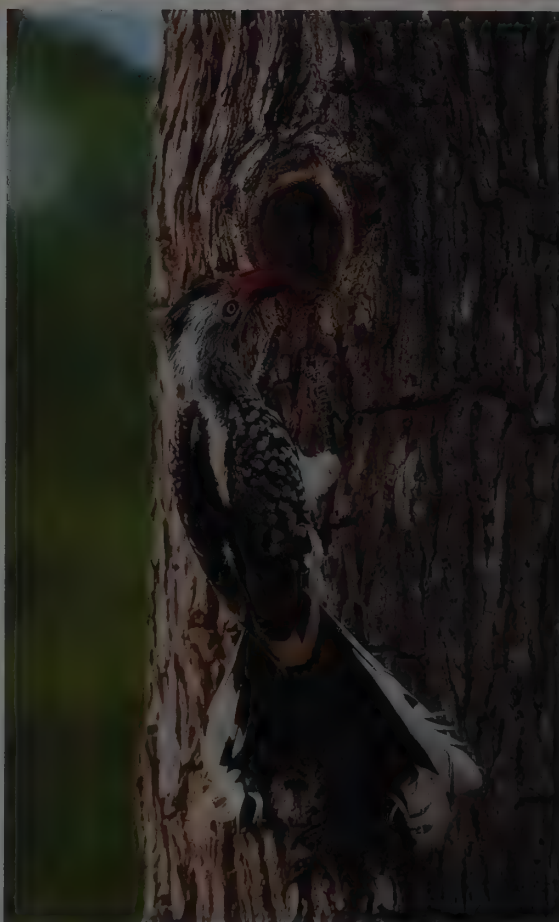


of the body, and finally draws the other wing and the tail along behind, all the while scrabbling with the feet on the rim of the entrance hole. The female and chicks fly immediately on emergence, and they do not re-enter the nest until a later season. The youngsters remain under cover near the nest for a few days or weeks, practising and developing the skills of flying, and being fed at intervals by their parents. They then join the adults on foraging expeditions, and they also start to develop further skills, or to play, using various types of behaviour such as wrestling with the bill, manoeuvring objects with the bill, or chasing high in the air and with twisting flight.

Nesting success has been recorded for only a few hornbills. For four small *Tockus* species in southern Africa, 90-92% of nesting attempts were successful in fledging at least some chicks. This was higher than the success rates of other hole-nesting birds in the same habitats, suggesting that a degree of protection was perhaps conferred on the nest by the sealed entrance. On the other hand, the proportion of chicks fledging from eggs that hatched was highly variable, ranging from 39% to 100%. This was due mainly to chick starvation, which depended on fluctuations in rainfall and associated food availability during the nesting cycle. In studies in Thailand, chicks fledged from 80% of nests of the Great Hornbill into which a female had been recorded to seal herself, while the corresponding figure for Austen's Brown Hornbill was 75%.

At the other extreme, the large Southern Ground-hornbills in Africa have been found to rear, on average, only a single chick per breeding group every nine to ten years. Individual groups varied in their breeding success, and fledging rates ranged from one chick once every two or three years to none at all in 20 years. Such a low annual productivity is balanced by an estimated annual turnover among adults, based on the replacement rates of the sexes within the study groups, of only 1-2%, but this still suggests that a long mean lifespan of 35-40 years is required for the study population to retain its current stability.

Records of longevity among hornbills come entirely from captive individuals. The longest-lived bucerotid on record is a female Great Hornbill, still alive at 41 years, and which laid its



In some areas nest-holes are at a premium, especially where trees are scarce, and artificial sites such as nest-boxes are rapidly utilized when provided. Von der Decken's and Red-billed Hornbills, in common with most hornbills of the seasonally dry forests of Africa, breed at the annual onset of the rains. Frugivorous species in tropical rainforests are less predictable, generally nesting only when fruit availability allows, and sometimes going two years without a breeding attempt. Unlike many hornbills, males in the genus *Tockus* sometimes provide assistance with nest-hole sealing, bringing the occasional lump of mud in the bill tip for the female to plaster around the cavity entrance.

In larger African species of the genera *Bycanistes* and *Ceratogymna*, males go one step further and swallow soil that is then formed into sticky pellets in the gullet and regurgitated to the female at the nest. Sealing of entrance holes can take anything from a few hours to a few days, and once the female is incarcerated a period of up to three weeks elapses before the eggs are laid. This is a rather remarkable fact, given that sperm in most birds is only viable for a few days at most. There is some evidence to suggest that glands in the female's oviduct nourish the stored sperm for the extra period. The obvious question of why females should choose to be sealed into a tree for a few preliminary weeks for no apparent reason is more difficult to answer, but it might be connected with ensuring propriety of the nest-hole.

[Above: *Tockus deckeni deckeni*, Kenya.

Photo: Bruce Davidson/Animals Animals.

Below: *Tockus erythrorhynchus rufirostris*, South Africa.

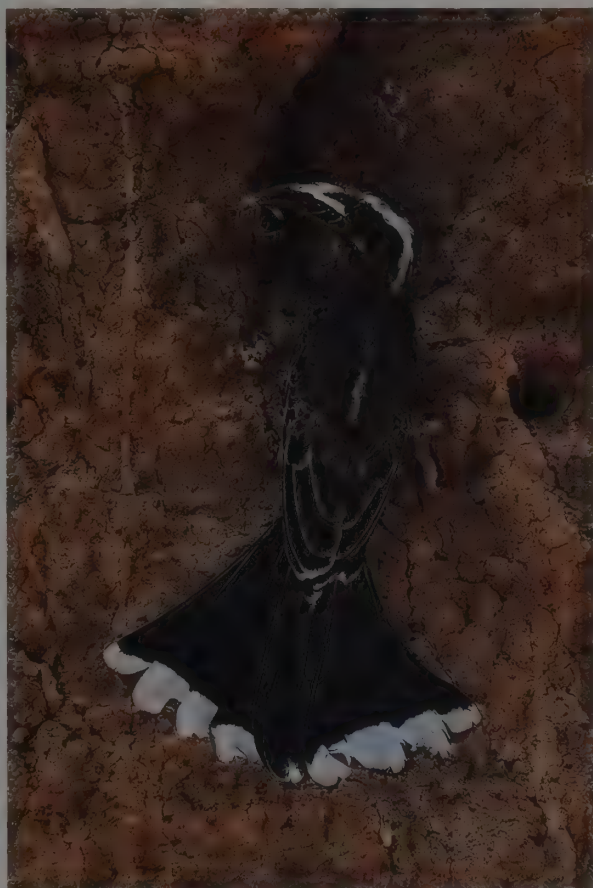
Photo: Ron O'Connor/BBC Natural History Unit]



After the bulk of the incubation period has passed the female usually breaks out of the nest and assists the male in feeding the brood. The female (left) African Grey Hornbill usually emerges when the eldest chick is 19–34 days old. In most species, the nestlings then reseal the cavity entrance using their own droppings and food scraps while the female joins the task of provisioning food. The differing moult strategies are well illustrated here, the female sporting a totally fresh set of remiges and rectrices which she has moulted and grown while sealed within the nest cavity. The male (right), meanwhile, possesses a very shabby set of wing and tail feathers that he is obliged to moult gradually.

[*Tockus nasutus nasutus*,  
Kenya.

Photos: Günter Ziesler]



first egg at the age of 39, while both individuals of a pair of Northern Ground-hornbills (*Bucorvus abyssinicus*), received as adults, were still alive 40 years later. Among the smaller species, an African Pied Hornbill (*Tockus fasciatus*) survived for at least 22 years, an African Grey Hornbill for 20 years and a Red-billed Hornbill for 18 years.

### Movements

None of the movements that have been described for hornbills appears to represent true migration, since the proportion of the population involved, and the exact direction taken, usually differ from one year to the next. The majority of hornbills are sedentary, and many are territorial. Those movements which do occur seem to be related more to fluctuations in food availability.

Some of the most frequent and regular movements are those made by species inhabiting deciduous African savanna and woodland. Once the trees in these areas have lost their leaves, the hornbills have, in effect, lost their habitat; they can no longer maintain territories, and so they form into flocks that wander in search of suitable new habitat. In West Africa, where the vegetation zones form a graded north-south series of relatively narrow belts, and where the main weather front oscillates across these belts, a reasonably predictable pattern develops. This apparently applies to a number of bird species, including the African Grey Hornbill and the Red-billed Hornbill, which move north at the start of the rains, in May-June, and return south at the start of the dry season, in October-November.

In other parts of their range, however, the same species either are sedentary, where this is permitted by a stable habitat, and are territorial throughout the year, or, where the habitat is less predictable, make erratic local movements only in some dry seasons. Generally, the drier, the more seasonal and the more marginal the habitat is, the greater will be the chance that the species will sometimes be nomadic. For example, Monteiro's and Bradfield's Hornbills, living in the most arid habitats occupied

by any hornbill species, appear to collect into wandering flocks at the start of every dry season. Nevertheless, even species of forest edge, such as the Crowned Hornbill (*Tockus alboterminatus*), are reported to wander far from their normal range during extreme droughts. Of special interest is a recent report of the mass drowning of hundreds of Red-billed Hornbills, as they attempted to fly across a branch of Lake Kariba, in Zimbabwe. It may have resulted from nomadic movements during a dry season, when the man-made lake perhaps blocked one of their traditional routes.

The other extensive movements made by hornbills are those undertaken by forest frugivores in search of fruiting trees. Even daily movements can be far-reaching, as suggested by the long distances over which birds travel each night to attend communal roosts outside the breeding season. Roosts may attract hundreds or rarely even thousands of birds, and Trumpeter, Great and Wreathed Hornbills fly in to them from at least 15 km away. It is also among these species that small flocks of non-breeding birds form, and these groups too are known to range over wide areas.

According to present knowledge, these movements in search of fruiting trees are all apparently erratic, but recent radio-tracking experiments have demonstrated that the large African *Bycanistes* species move at least 160 km during the course of one year. Some Asian species are also suspected of wide-ranging movements. It has already been shown that Wreathed Hornbills, for example, cover at least 100 km<sup>2</sup> in one day of foraging, fly to offshore islands, as between Java and Bali, and cross 30 km of open country. Some of these movements may prove to be regular and predictable once the pattern of fruiting trees is known on a larger geographical scale.

### Relationship with Man

In many countries, wild-living hornbills are so large and obvious, and have such unusual nesting habits, that they attract people's attention and have often been incorporated into local





*In the Great Hornbill, care of the female once she has sealed herself into the nesting cavity is the sole responsibility of the male. The task is a protracted one, as females in this species can remain confined within the nest for as long as four months or more, while the processes of laying, incubation, hatching and the development of the chicks are carried out. During the period when the chicks are growing, the male may bring as many as 185 food items per day to the nest. Note the ochre staining on the wings and neck of this male, the result of a secretion of coloured oils from the preen gland (itself marked by a spot of ochre on the rump). Such staining shows great individual variation, and commonly also affects the tail as well as the bill and casque.*

[*Buceros bicornis*,  
Khao Yai National Park,  
Thailand.  
Photo: Tim Laman]

cultures, folklores and ceremonies. They are also large enough to make a good meal, which renders them appealing targets for hunters, who may also open the nest or cut down the nest tree in order to collect the breeding female and chicks. This robbing of nests has a further application, since live hornbills also provide attractive exhibits in captivity, can become very tame and make interesting pets. This has led to captive hornbills not only being kept by indigenous peoples, but also being exported to other parts of the world to be housed in zoos and private avicultural collections.

In Africa, the large ground-hornbills have received the most attention. Both species are frequently recognized as having a totemic function, and are often respected by the local people. In West Africa, the sound of hornbill calls, as well as carvings or effigies of these birds, are widely involved in local mythology, plays and dances. Among some African tribes, in at least Nigeria, Cameroon and Sudan, the head and neck of a Northern Ground-hornbill, attached to a headband and worn as a camouflage, has been sported by groups of hunters, crouched and black-

skinned as they stalk a herd of antelope or other game. In Gambia, however, the same ground-hornbill species is regularly disturbed, since it is considered bad luck if not seen in flight. Among some southern African tribes of Zulu and Xhosa origin, the Southern Ground-hornbill is used in an attempt to break droughts, a carcass of the bird being tied in a streambed in the belief that it will attract rainwater, which will wash away the dirt associated with the hornbill's habit of enclosed nesting. Parts of the same species are also taken as a tonic to improve health and sagacity, and the demand for this remedy, and the high value placed on it, have made this species vulnerable to overexploitation.

Since the sexes of both species of ground-hornbill utter deep, booming calls as duets, these sounds are often reflected in onomatopoeic local names or are rendered, at least in southern Africa, by various sayings. One such commentary has the female saying "I am going, I am going, I am going home to my relations", to which the male answers "You can go, you can go, you can go home to your relations". Another anthropomorphic story tells how a ground-hornbill visited his in-laws, who were mov-





Newly hatched hornbill chicks are blind and practically naked.

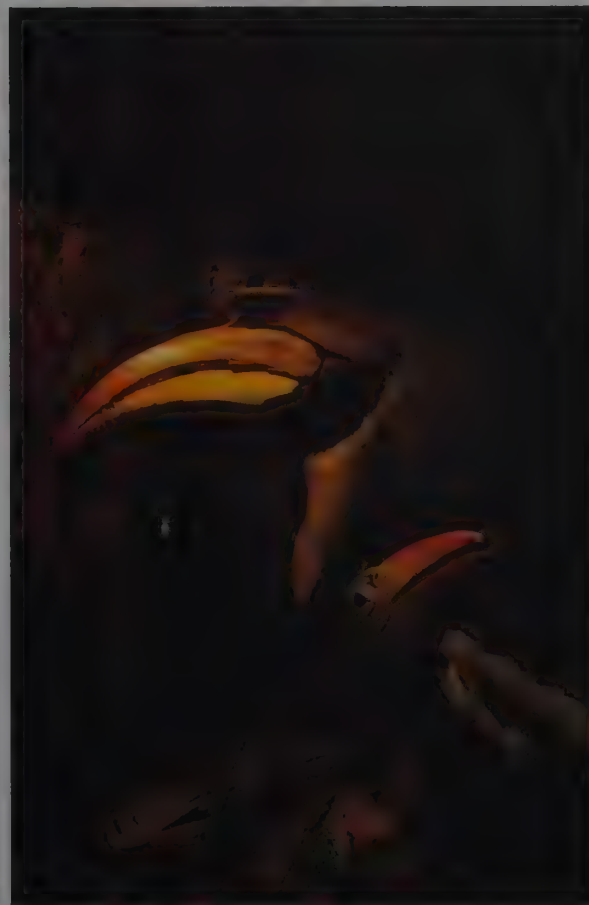
They are fed from the outset with whole food items of varying sizes.

In larger species, such as the Great Hornbill, the skin of the chick changes from pink to dusky after around one week.

At 10 days or so, the eyes open and the feather quills protrude from the skin, the barbs themselves not breaking out for some considerable time so that the young hornbill (in common with many other coraciiform species) spends a short while in the nest looking rather like a porcupine. At this early stage, however, the legs of the nestling are well developed and allow it to stand freely in the nest and clamber to squirt its droppings from the entrance.

These photographs show the male arriving at the nest, regurgitating a food item to the tip of its bill and passing it to the female through the slit. She then transfers the item to the chick which begs vociferously.

In the last photograph of the sequence, the moulted wing and tail feathers of the female can be seen strewn around the nest cavity.



[*Buceros bicornis*,  
Khao Yai National  
Park, Thailand.

Upper photos:  
Morten Strange

Lower photos: Tim Laman]





The hornbill family contains a high proportion of species that live as co-operative groups. Such groups generally consist of a dominant pair of breeding adults that are assisted by helpers, with up to 20 individuals in a single group. Helpers are often adult males or immature birds from the previous breeding attempt, but in some species helpers of both sexes appear to be equally common. All group members contribute to territory defence and the provision of nest lining material and food. Eight species of hornbill are confirmed co-operative breeders, including the Sulawesi Tarictic Hornbill, pictured here, while another ten are suspected of employing this breeding system at least occasionally. This nest amongst the root system of a strangler fig (*Ficus*) contains a female inmate and is attended by a dominant male, a helper male and a non-breeding female. Helpers in co-operative groups probably receive reproductive benefit by one of three main processes. First, they might opportunistically copulate with the laying female, a possibility suggested by the jealous mate-guarding behaviour shown by dominant males. Second, they may well be related to the dominant pair and thus assist in passing on a fair proportion of their own genetic material. Third, group membership presumably improves the likelihood of eventual dominance and therefore breeding, in the case of, for instance, the death of the dominant male.

[*Penelopides exarhatus exarhatus*,  
Tangkoko DuaSudara  
Nature Reserve,  
Sulawesi.  
Photos: Tui De Roy]





ing to another location; the obliging bird willingly allowed a load to be put on his back, saying that he would transport it, but when the time came to leave he was unable to fly because of the extra weight. The bird's call is said to mean "It's too heavy, I can't take off with this load on my back". The Shona-speaking people have a customary adage that those who cannot say no to others are like the ground-hornbill.

In many regions, hornbills are closely associated with the medical, mythical and religious traditions of local people. In India, the Great Hornbill and the smaller Indian Pied Hornbill (*Anthracoceros coronatus*) and Indian Grey Hornbill are boiled up for medicinal purposes, the resulting concoctions being related especially to childbirth and life after death. Throughout the Indian Subcontinent and South-east Asia, it is chiefly the *Buceros* hornbills that have been most frequently absorbed into many myths and rituals. Skulls, casques and tail feathers have been, and still are, incorporated into head-dresses, ear-rings and feathered capes by peoples of India, Peninsular Malaysia, Borneo, Sulawesi and the Philippines. All four of the huge Asian species, comprising the three *Buceros* and the Helmeted Hornbill, have been involved in these traditional practices at various times and in various localities, as also has the Knobbed Hornbill (*Aceros cassidix*). This use of hornbills has a long and particularly active history on the island of Borneo. Here, the antics of hornbills, as they bounce on their perch or dip the head, are incorporated into several important dances, while the Rhinoceros Hornbill is the focus of a ritual enacted by indigenous people of Iban or Dyak descent. This ceremony, called *gawai kenyalang*, involves the carving of large, elaborate and symbolic hornbill effigies, and the use of the white tail feathers with their black bar in head-dresses, capes and dancing fans. In times past, the effigies were associated with the god of war, and the purpose of the *gawai kenyalang* was to summon this deity, offer him food and gifts, and then send him to kill the souls of the offending enemy, usually a neighbouring tribe. Success in the latter, more important objective was ensured by raising the decorated Rhinoceros Hornbill effigy high on a pole, thus launching the attack of the war god. The beak and curled casque of this species also appear regularly as a motif in Bornean sculpture and painting, decorating anything from cabins to coffins and canoes, and even as tattoos adorning tribal men and women.

The use of tail feathers of the Helmeted Hornbill and the Rhinoceros Hornbill, particularly the elongated central pair of the former species, is also frequent in Bornean rituals. Nowa-

days, one longhouse may own only one set of these feathers, mostly kept carefully stored between wooden slats, and taken out for special occasions or rituals during which a male dancer wears a feathered skullcap and a goatskin or leopard-skin dancing cloak adorned with tail feathers of these two hornbills. The feathers billow black and white when he dances. Another dance involves Kenyah women slowly turning, their feet stamping to mandolin music, while their swaying hands whirl fans of hornbill feathers.

The role of the Helmeted Hornbill in local rituals has in the past been confused by the additional use of the solid ivory casque as an ancient trading item, prized by the Chinese. In Ming Dynasty China, hornbill ivory, known as *ho-ting*, carried a commercial value far in excess of elephant ivory or jade. It was used to create a variety of ornaments, including carved "magic horses", plume-holders, snuff bottles or exquisite mandarin belt buckles which only high-ranking officials were permitted to wear; the rich orange colour of the preen oils was probably retained by a process of heating and pressing of which no detailed description survives. The block of hornbill ivory was also employed as a medium for delicate and elaborate carvings of ornamental scenes, often kept intact with the skull, which was itself decorated with coloured feathers or other items. The local Kayan, Kenyah and Kelamantan peoples of Borneo, who so valued the tail feathers, also use the casque to make roughly carved ear-rings or ear-plugs, as well as toggles and buckles for belts and swords. Although the trade to China has ceased, the collection, trade and sale of hornbill artefacts continues to this day in Borneo, at least, although it appears to be decreasing.

In more modern contexts, hornbills are also featured as regional or local emblems. The Rhinoceros Hornbill is the national emblem of the Malaysian State of Sarawak, and appears prominently on its coat of arms. Sarawak promotes hornbills as one of its main tourist attractions, advertising "Sarawak - Land of Hornbills", and displaying hornbill artefacts as part of ritual dances performed for visitors to longhouses. In Indonesia, the Knobbed Hornbill is the emblem of South Sulawesi Province and the Helmeted Hornbill that of West Kalimantan Province.

### Status and Conservation

It is reasonable to say that hornbills have long been declining across their entire range, since the habitat changes wrought by

Austen's Brown Hornbill is a co-operatively breeding species in which the dominant male and all other male group members provision the female when she is incubating and brooding. In the left-hand photograph, male helpers wait their turn to feed the imprisoned mother and young. In the right-hand one, the female, identifiable by her dusky throat, is showing food to the fully grown nestling, in an attempt to encourage it to leave the nest; the male and the helpers watch expectantly and indeed often assist in this task.



[*Anorrhinus austeni*,  
Khao Yai National Park,  
Thailand.

Photo: Atsuo Tsuji/  
Thailand Hornbill Project]

man are rarely beneficial to the members of this intriguing family. For thousands of years, humans have altered the habitats occupied by hornbills through the agency of fire and axes among savanna, forest and woodland. It is only with the emergence of an industrialized consumer society, however, that habitat alteration has proceeded at such a pace that it places hornbills, as well as many other species, at risk. The factor influencing the status and conservation of the largest number of bucerotid species is undoubtedly deforestation. The removal of forest has been accelerated by the introduction of various mechanical techniques and by increases in human population pressure, resulting in greater access along forestry roads, improved hunting methods, the spread of shifting cultivation, and such undesirable side effects as widespread forest fires. There are two crucial factors underlying the vulnerability of hornbills to deforestation: one is the tendency for nest-holes of sufficient size to occur in large trees, and another is the fact that large trees are preferentially targeted by logging operations. Since the majority of hornbill species live in forest, and because they are unable to withstand the removal of all large trees from such areas, or to persist in degraded habitats, most of them are in decline. This also means that the most highly threatened of the Bucerotidae occur in South-east Asia, where almost all species occupy forest habitats.

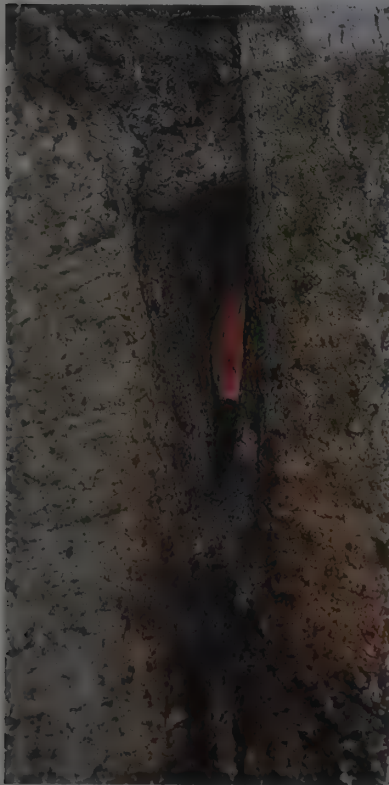
Another factor increasing the susceptibility of Asian hornbills to extinction is the small total range of a number of species. Some have evolved on single islands or archipelagos and are constrained by the available land surface. As a consequence, they have relatively small populations, and no alternative areas to which they can retreat should their restricted habitats be adversely affected or removed. In Africa, on the other hand, about half of the species are widespread in savanna, and even those confined to forest have wide distributions within forested habitats. A further problem related to small population size arises for the large species of hornbill, since they often occur at very low densities and so require extensive areas of habitat just to support viable populations. It has been estimated that at least 2000 km<sup>2</sup> of tropical rainforest or 50,000 km<sup>2</sup> of savanna are necessary to support a population of about 500 breeding pairs of the largest hornbill species. Such extensive tracts of natural habitat are becoming rarer every year.

Of the 54 species of hornbill, no fewer than nine are currently considered threatened, all of them from the Oriental Re-

gion, as are ten of the twelve Near-threatened species. Seven of the threatened species are restricted to small oceanic islands: the Palawan (*Anthracoceros marchei*) and Sulu Hornbills (*Anthracoceros montani*); the Visayan (*Penelopides panini*) and Mindoro Tarictic Hornbills (*Penelopides mindorensis*); the Rufous-headed Hornbill (*Aceros waldeni*); and the Narcondam (*Rhyticeros narcondami*) and Sumba Hornbills (*Rhyticeros everetti*). The Sulu and Rufous-headed are classed as Critical; the two *Penelopides* species as Endangered; and the remaining three as Vulnerable. Of these seven, one species is Indian and one Indonesian, whereas an alarming five are Philippine.

Narcondam is a remote island lying in the Andaman Sea between the Andaman Archipelago and the coast of southern Myanmar. It is only 7 km<sup>2</sup> in extent and supports populations of few bird species, including a single endemic, the Narcondam Hornbill. Given the small size of the island, the total population of this bird must always have been tiny, even though it is reportedly much the commonest bird present. Estimates have ranged from 200 to 400 individuals, with the most recent assessment, in 1998, concluding that 295-320 individuals inhabited Narcondam. While this bird has long been protected by the isolation of its range, times have changed on its island home. A permanent police post was established in 1969, and goats have been introduced. The first factor has led to minor habitat loss and hunting for food, with around 25-40 hornbills killed annually, while the second has denuded the undergrowth and apparently eliminated seedlings of the fig trees that provide the main food source and nest-sites for the hornbills. As the population of this species is so small, it is susceptible to natural disasters such as cyclones and disease, and any reduction in its numbers is dangerous. The establishing of a second population on another islet in the Andamans has been proposed, but this is ecologically risky, and it is probably far more important to boost the resilience of the Narcondam population by exterminating goats, planting extra fig trees and providing nestboxes.

Closed-canopy forest on the Indonesian island of Sumba has declined in extent through the twentieth century and now covers only an estimated 1732 km<sup>2</sup>, mostly in small patches. These areas now support an estimated population of about 4000 Sumba Hornbills, but the forest is continually being reduced by wood-cutting and eroded by grass fires at its periphery. Large, isolated



The first task for the aspiring fledgling is to break down the sealed walls of the nest entrance (or exit in this case), frequently a protracted process that involves long periods of patient pecking. It can take anything from a few hours to several days for the process to be completed. Having completed the task, this young Crowned Hornbill emerges from the narrow aperture of the nest cavity. Its flight becomes efficient very quickly, although noticeably less skilful than that of its parents.

[*Tockus alboterminatus*, Eshowe, KwaZulu-Natal, South Africa. Photos: Peter Steyn]





The first flight is a crucial moment in any bird's life, as it is a time when many things can go wrong, when the young bird is highly vulnerable. After having worked hard to enlarge the opening to its seemingly impregnable nest-hole, this Great Hornbill chick manages to clamber out, ready to face the outside world.

Typically, the bird will initiate its exit by sticking its head through the enlarged hole, after which one wing follows. What usually amounts to a spell of scrambling and pushing with the feet ensues, then the other wing and the body are eased through the gap, the tail following without difficulty. After all the effort involved, this chick is unfortunate and flops to the ground, whence it will find take-off a good deal more difficult, and where it is particularly at risk from all sorts of predator. During the entire process of emergence, the adults tend to perch nearby watching, but powerless to help. One Great Hornbill chick was recorded taking two days to emerge from its nest-hole, ending up dirty and exhausted after its ordeal, but nonetheless successfully out in the open. Once emerged, the young birds tend to stay near the nest for some days or weeks, being fed by their parents, and gradually learning the skills they need for ultimate survival.



[*Buceros bicornis*,  
Khao Yai National Park,  
Thailand.  
Photos: Atsuo Tsuji/  
Thailand Hornbill Project]



After fledging, juvenile hornbills are closely accompanied by their parents for some time. Gradually, they start accompanying the adults when these set off in search of food, and they continually develop their skills with a variety of activities, such as wrestling with their bills, or aerial chases with increasingly agile flight manoeuvres. In co-operative species, like the Bushy-crested Hornbill, the young birds often remain within the group long after maturity. Males tend to stay with groups longer than do females, and they are more likely to end up becoming helpers.

[*Anorrhinus galeritus*,  
Gunung Palung  
National Park,  
West Kalimantan, Borneo.  
Photo: Tim Laman]

fig trees are being removed to make way for agriculture, and the hornbills are still being hunted for food and local trade. As part of the Sumba Forest Conservation Strategy, fieldwork was targeted at identifying potential reserves for the species, and, as a result, two new national parks totalling 1350 km<sup>2</sup> were created in 1998. It is hoped that these will help to protect some of the island's remaining tracts of forest and, thus, its endemic hornbill.

In the westernmost Philippines, several islands in the Palawan and Calamian groups harbour populations of the Palawan Hornbill. The number of individuals surviving is unknown, but the figure is apparently small, and is certainly dwindling owing to high hunting pressure and the inexorable diminution of forest cover within the hornbill's restricted range. The species occurs in St Paul's Subterranean River National Park on the Palawan mainland, and its survival depends on the effective conservation of this protected area and the establishment of further suitable reserves.

As well as ranking among the most poorly known hornbill species in the world, since neither the main call of the adult nor the bare-part colours of the juvenile have been adequately described, the Sulu Hornbill is perhaps the rarest. It is known from only three small islands in the Sulu Archipelago, in the south-west Philippines, where, judging from the reports of a nineteenth-century expedition to the area, it was evidently once common. There have been very few recent sightings, however, and it is thought to persist only on the main island of the Tawitawi group. The number of hornbills surviving there is unknown, but an alarmingly low estimate of under 20 on the island's main mountain range has been made. A rapid increase in illegal logging on Tawitawi, coupled with intensive and uncontrolled hunting for food and, apparently, target practice, poses a severe threat to the species. Some nests are raided annually by villagers, who eat or sell the nestlings. To make matters worse, the area is politically unstable, and conservation work is hampered by the activities of extremist groups and militias. If measures are not taken soon to counteract these pressures, the Sulu Hornbill may well vanish within decades.

All four of these species are at high risk, none is known to have bred successfully in captivity, nor are any live specimens maintained in any major conservation collections. It is clear that

much work remains to be done before the future of these species can be considered secure.

The general situation is similar for the other threatened species endemic to the Philippines, where the problem of habitat loss is compounded by both taxonomic and demographic uncertainty about the populations involved. For example, if the populations of *Penelopides* in the Philippines comprise at least four species rather than just one (see Systematics), then there are two species gravely at risk, the Visayan and Mindoro Tarictic Hornbills; indeed, both are currently considered Endangered. Even more worrying is the situation of the Rufous-headed Hornbill, the more so if it is treated as a separate species from the Wreathed Hornbill (*Aceros leucocephalus*); while little is known of its general habits and behaviour, it is clear that much of the forest habitat on which it is reliant has disappeared, and its global population has been estimated at under 100 pairs. The fact that the few remaining birds congregate at favoured fruiting trees renders them highly susceptible to hunting. In one extremely sad incident in 1997, around 40 hornbills, not all of this species but probably including more than a quarter of the entire north-west Panay population of the Rufous-headed Hornbill, were shot in a single day, resulting in a major local feast and with excess meat sold at market stalls. It is easy to visualize how rapidly this species could meet its demise if a single hunting event can eliminate such a large proportion of the population. The Rufous-headed Hornbill's situation is therefore regarded as Critical, and it is the main focus of a current conservation project in the western Visayan Islands. Regardless of any taxonomic uncertainty, at least three distinct subspecific populations of tarictic hornbills have been lost or are close to disappearing from the islands of Basilan, Polillo and Ticao in the Philippines. Each of these islands is already deforested and unlikely to support any hornbill populations.

Hornbills of several species have also declined markedly throughout the very large islands of Sri Lanka, Sumatra, Java, Borneo and Sulawesi. None of these is currently categorized as threatened, because their populations are too large and their rate of decline too slow to meet the relevant criteria. Although the Indonesian islands are currently suffering extremely rapid clearance of lowland forest through fire and logging, most hornbill



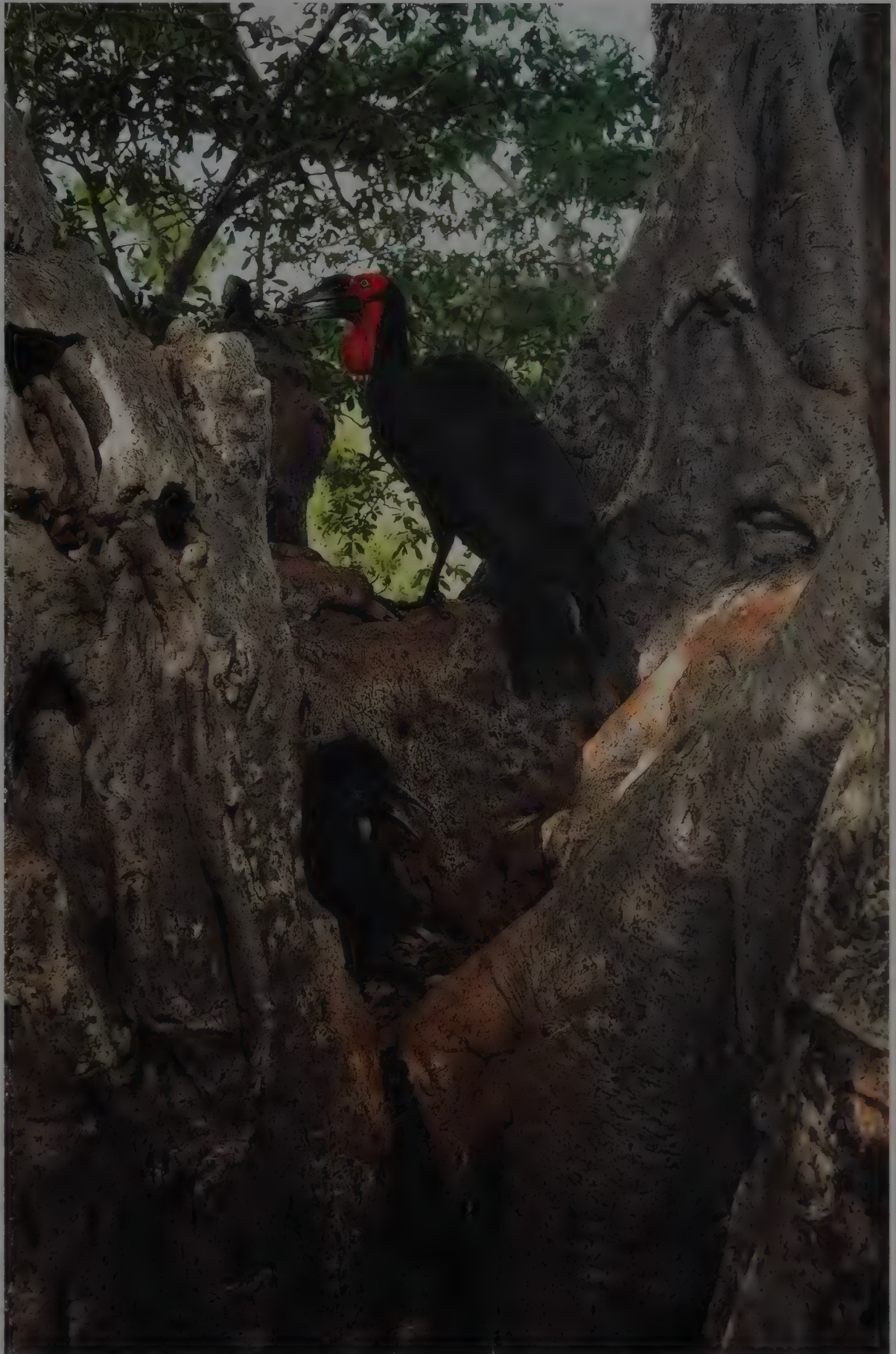
The nest of the Southern Ground-hornbill is usually situated in the cavity or crook of a large tree or rock face. On rare occasions, the abandoned stick nest of another species is used or a cavity is dug out of an earth bank. This is the only species in which hornbills have been recorded excavating their own nest-hole. As seen here, the male regularly adds dead leaves to the nest lining.

As with most hornbills, the dominant female undertakes all incubation duties, but there is a major difference in nest design: no attempt is made to seal the nest entrance, and the female is free to come and go as she pleases. Two eggs are laid, these hatching asynchronously with the younger sibling usually dying of starvation after a short while, but presumably surviving in times of plenty.

After fledging, the juvenile remains with the group until maturity, and perhaps for considerably longer. As with most co-operative breeding species, it is the females that more rapidly leave their natal group and seek prospective mates elsewhere.

Other peculiarities of ground-hornbill breeding behaviour are that they overlook nest sanitation, leaving their droppings in the nest rather than squirting them out, and females moult like males, presumably because their need for flight is undiminished during the nesting cycle. Breeding turnover in this species is extremely slow with an average of one chick recorded from each breeding group every nine or ten years. The actual rates recorded to date varied from one chick every two to three years to no young produced by one group in 20 years. Given turnover in the adult population of only 1-2% per annum, recruitment will be sufficient if the average lifespan is in the order of 35-40 years.

[*Bucorvus leadbeateri*,  
Kruger National Park,  
South Africa.  
Photo: Tim Laman]







populations extend well up into the more secure hill forest and it is this that provides most hope for the future.

Populations of hornbills on the Asian mainland are, for the most part, less vulnerable in a global sense because they occupy much larger ranges. Nevertheless, most species have declined or disappeared in several regions or countries, often resulting in patchy distributions that make any assessment of population size and viability difficult. For example, the Great Hornbill is apparently widespread in Myanmar and Thailand, uncommon in Malaysia and Sumatra, but evidently threatened in India, Laos and Vietnam.

Only two continental species are considered threatened. One of these, the Rufous-necked Hornbill, is currently classified as Vulnerable: it is extinct in Nepal, notwithstanding its scientific name, and it has disappeared from much of its previous range in north-east India and Thailand, while it appears to be very rare in most of its wide distribution in China, Myanmar, Vietnam and Laos. Deforestation is at least partly to blame for its decline, but the principal threat is posed by hunting. Large areas of forest remain in the montane range of this species, but the people who share these forests are, with the exception of the Bhutanese, great hunters, and hornbills are one of their favourite targets. This species, along with other hornbills, disappeared from Doi Suthep in northern Thailand as a direct result of hunting pressure, and the same process is occurring gradually throughout South-east Asia. The Rufous-necked Hornbill receives protection in Huai Kha Khaeng Wildlife Sanctuary in west Thailand and in Namdapha National Park in India, while two major populations offer hope for its long-term survival. One of these is in the Himalayas of Bhutan, and the other in the Annamite Mountains of Laos.

Tickell's Brown Hornbill and the Plain-pouched Hornbill were formerly thought to be subspecies or age-classes of other bucerotids, but both have been elevated to the taxonomic level of full species (see Systematics). Although they have relatively small ranges, centred across the Myanmar-Thailand border, the larger species is considered Vulnerable and the smaller only Near-threatened. This is merely because Tickell's Brown Hornbill is usually treated as conspecific with Austen's Brown Hornbill; if accepted as a full species in its own right, as seems justifiable, it would surely qualify as threatened. Both species are in large part reliant on a few protected areas in west Thai-

land, principally Huai Kha Khaeng Wildlife Sanctuary, Bung Kroeng National Park and Khaeng Krachan National Park. Huge numbers of Plain-pouched Hornbills were once found in southern Myanmar, particularly in the northern Mergui Archipelago and the Sittang Valley. Little is known about these populations at present because of the difficulty of access in a politically unstable region, but no hornbills were seen during a recent visit to Toungoo, a town around which the species once abounded. If forests remain in Mergui and in the hills of southern Tenasserim, it is to be hoped that both the Plain-pouched Hornbill and Tickell's Brown Hornbill will be found to survive in the area, especially in the recently established Myinmoletkat Biosphere Reserve, but the current options for conservation in Myanmar are few.

On the basis of this evidence, the outlook for the Plain-pouched Hornbill was apparently fairly bleak, until, that is, a rather remarkable discovery was made in the forests of Perak, in northern Peninsular Malaysia, by H. C. Ho and S. Sutari. Large numbers of hornbills were seen repeatedly travelling to roost-sites near the Perak River, and these were presumed, understandably, to be Wreathed Hornbills rather than that species' rare cousin, which was struck off the Malaysian bird list in the 1970's owing to lack of evidence of its occurrence in that country. Investigations finally confirmed, however, that the species involved was the Plain-pouched Hornbill, and it has subsequently been located by members of the Thailand Hornbill Project in extreme southern Thailand. These findings raise hopes that this species could be more common and widespread than was recently feared, and that extra protection might be forthcoming from Hala-bala Wildlife Sanctuary in Thailand and the Temenggor-Belum Sanctuary in Malaysia, so long as the constant threat of logging can be held at bay.

Other species in Asia have a wide range within which they show rather specific habitat requirements. This means that, even though they remain widespread, they could become rare. The Wrinkled Hornbill is an example of such a species. It favours lowland forest, including swamp-forest and peat-forest, which are now by far the most degraded forest types across its entire area of occurrence. The species currently appears to be rare throughout its range, and there is concern about the long-term resilience of such a sparsely distributed population. In a similar way, the Helmeted and White-crowned Hornbills are becoming rarer within their preferred foothill habitats.

In Africa, hornbill species have suffered only local declines or extinctions. Africa is also fortunate in that relatively large tracts of forest and savanna have been conserved as national parks or other conservation areas. The most vulnerable populations appear to be those of the West African forest, which has suffered greater deforestation per unit area than has any other forested region on that continent. The Yellow-casqued Hornbill is the only bucerotid restricted to this part of Africa, where its relatively low density coupled with its large size must be seen as reason for concern. It is currently considered Near-threatened. The nominate race of the uncommon Brown-cheeked Hornbill may warrant elevation to the status of a full species, in which case it would become a second endemic species of the West African forest and its reclassification as Vulnerable would probably be fully justified. In addition, some other forest-dwelling hornbills have distinctive races confined to the West African forests.

Other Afrotropical hornbills that have restricted ranges do not appear at present to be at risk. In south-west Africa, Monteiro's and Bradfield's Hornbills still have large tracts of good-quality habitat available to them, and they appear not to be declining. In north-east Africa, Hemprich's Hornbill is similarly widespread and locally common. All the remaining African bucerotids occupy very extensive ranges, and many of them are small species, so that each is very likely to persist in relatively large populations. Local reductions in range are probably a common factor for a number of species, but are of conservation concern only for the large species that occur at low densities. In West Africa, the big *Ceratogymna* hornbills are always the first to disappear from disturbed habitats, mainly as a result of increased hunting pressure. In South Africa and parts of Zimbabwe, the Southern

*While it is not currently classified as threatened, Bradfield's Hornbill occupies one of the most restricted ranges of all continental hornbills. It occurs in Baikaea-Guibourtia-Pterocarpus woodlands on sandy soils, extending to adjacent drier forests including those dominated by mopane (Colophospermum). These habitat types are restricted to a relatively narrow belt across south-central Africa, and the species is therefore confined to this region. It remains locally fairly common, but its small range makes it potentially vulnerable to the current degradation of its favoured habitat.*

[*Tockus bradfieldi*, Chobe, Botswana.  
Photo: Jacques Gilliéron]

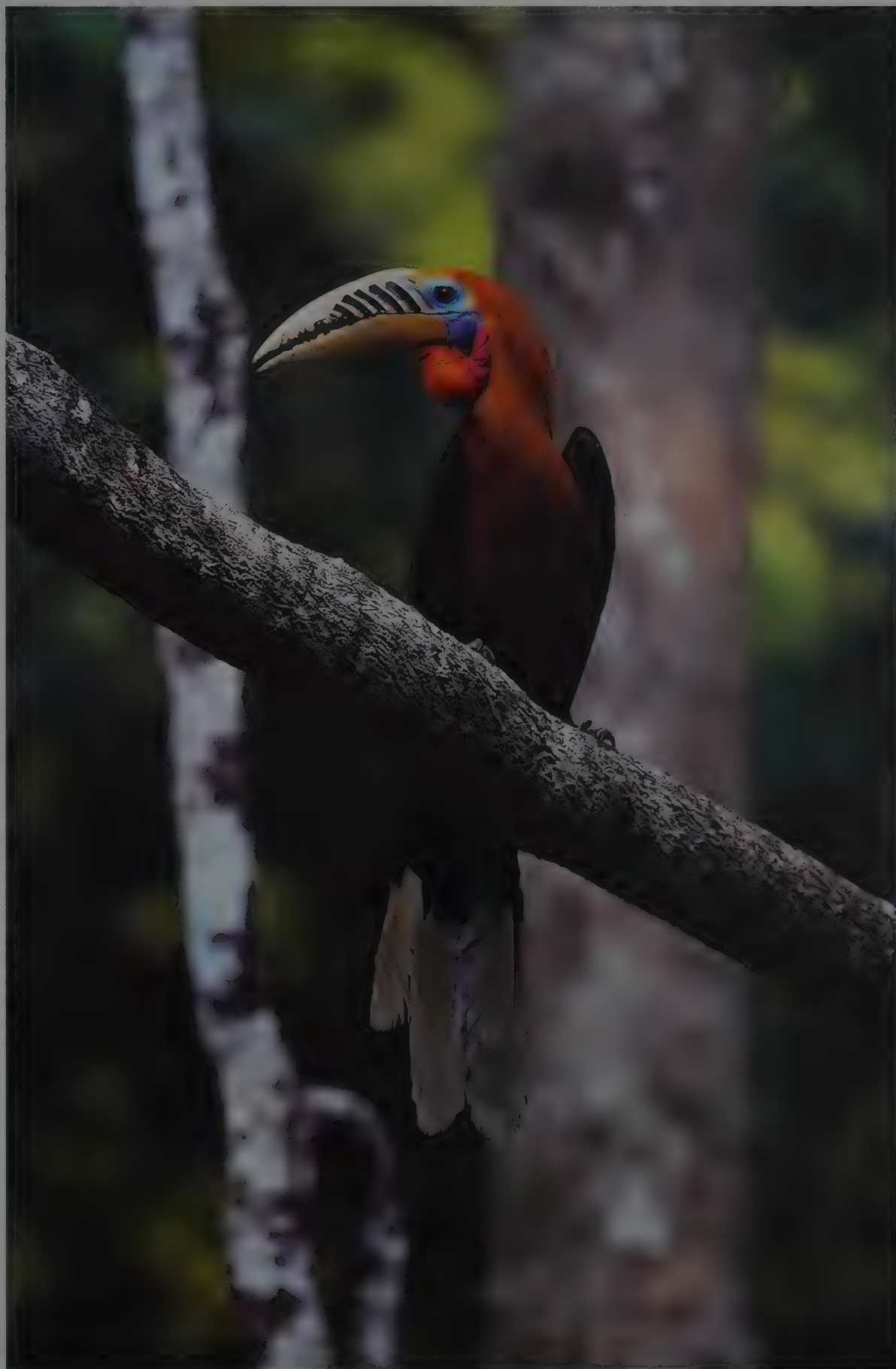


Once widespread in montane forest from Nepal to Vietnam, the Rufous-necked Hornbill has declined almost throughout, and is now extinct in many areas.

For example, on Doi Suthep, in northern Thailand, a once large population has been completely extirpated. The factors underlying this widespread decline are essentially twofold: loss of habitat has been extensive; and hunting pressure has been extreme. Hornbill meat is much sought after in rural areas, particularly in montane regions of Southeast Asia and this species is especially vulnerable as its range overlaps those of hill-tribes such as the Nagas, Karens and Hmong, whose lifestyles are heavily reliant on subsistence hunting.

There remain three large populations of the species particularly worthy of protection: one survives in Bhutan, including Thrumshingla National Park; another in Arunachal Pradesh, including Namdapha National Park; and another remains around Nakai-Nam Theun National Biodiversity Conservation Area, in the Annamite mountains of Laos. The species is often first detected by a deep abrupt "gok", that is regularly given by flying or foraging birds throughout the day.

[*Aceros nipalensis*,  
Huai Kha Khaeng Wildlife  
Sanctuary, Thailand.  
Photo: Tim Laman]





The Rufous-headed Hornbill survives only on the islands of Panay and Negros, in the Philippines. There are quite possibly fewer than 100 adults of this species left, and numbers continue to decline owing to habitat loss and heavy hunting pressure. In one recent heart-breaking incident 40 hornbills, including a large proportion of the global population of this species, were shot at a single fruiting tree in a single day on Panay. Losses of this severity are clearly unsupportable and, if left unchecked, will bring the demise of the species in the next few decades. The main hope lies in a conservation programme currently operating in the Visayas, with the Rufous-headed Hornbill as its main target.

[*Aceros waldeni*,  
Hamtang Forest,  
Panay, Philippines.  
Photo: Jon Hornbuckle]

Ground-hornbill has lost about 70% of its previous range and is now common only in large conservation areas.

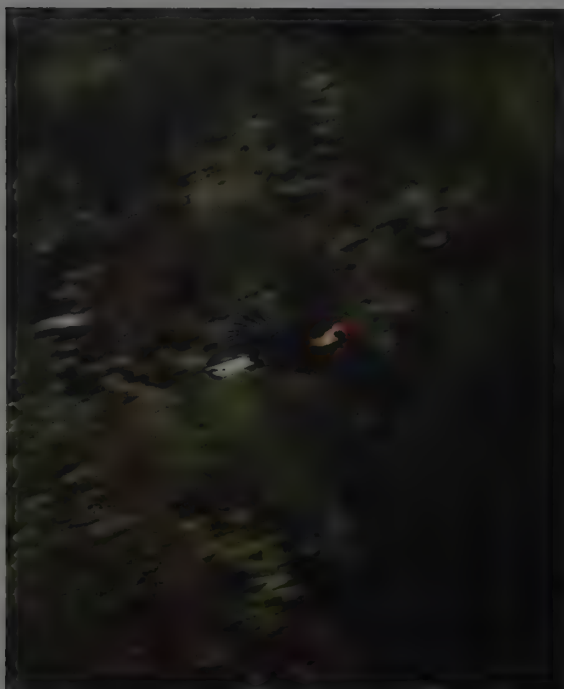
Apart from habitat alteration, the main threats to hornbills come from hunting for food and traditional medicines, and the robbing of nests for food or for the avicultural trade. The extent and impact of these problems is difficult to determine, but their effect on hornbill populations is all the more serious because these are long-lived birds with a slow rate of population turnover and recruitment. The hunting of hornbills has undoubtedly been taking place for centuries, but its effect has increased markedly with the use of firearms, and with improved access to forest along roads built for logging and development pur-

poses. In West Africa and in parts of India, Thailand, Malaysia and Indonesia, and probably elsewhere, too, declines in the populations of several hornbill species have been attributed directly to hunting pressure and to the collection of females and chicks from nests. In much of South-east Asia, wildlife is preferred over domestic livestock as food, and hunting in forests is therefore rife. Unfortunately, hornbills are quite tasty and are considered a delicacy in, for example, Laos and Vietnam. It is not surprising, therefore, that in accessible areas of these countries all bucerotids are conspicuous by their absence. Some hornbills are easy to hunt because they respond to whistled imitations of their calls, a behavioural trait used to advantage by forest-dwelling hunters, who have learnt to attract hornbills within range of their weapons. In Borneo, a single team of traditional dancers requires around 400 Rhinoceros Hornbill tail feathers, and thus the demise of 40 or more birds. This demand, and that for hornbill meat and casque ivory, was shown to exceed the calculated sustainable level of hunting of one bird killed per 25.6 km<sup>2</sup> per year, with the effect that several species were declining, or becoming locally extinct, in Borneo. As a result of hunting bans, or a decrease in hornbill availability, an increase in the use of artificial tail feathers in Bornean rituals has been reported. Elsewhere, the avicultural trade in hornbills continues to meet the demand for these birds as pets and zoo exhibits, despite the positive effect of international controls on the transportation and importation of hornbills into countries outside their original ranges. In only a few local instances have other factors been implicated in declines. These have included the poisoning of ground-hornbills, and the persecution of these birds for breaking windows after they had made territorial attacks on their reflections.

On a more positive note, it has been shown that a number of forest hornbills are able to forage successfully and survive at reasonable population densities within selectively logged or secondary forest. Several savanna species also feed in degraded habitats. The main problem in these instances is that suitable large trees to provide nesting cavities are often absent, or limited in number. In some cases, such as that of Southern Ground-hornbills in agricultural areas of eastern South Africa, the presence of rock faces still ensures a supply of safe sites for roosting and nesting. The provision of nestboxes has been widely tested only on small *Tockus*

The forests of Mindanao, over which this male Wreathed Hornbill is flying, are disappearing with alarming rapidity, as they are throughout the Philippines and to a greater or lesser degree throughout Africa and Asia. This is the major factor underlying the decline of hornbill species such as this, but with high levels of hunting and trapping for trade also depleting populations, the future for many hornbills is bleak. While the Wreathed Hornbill is thought to remain too common for classification as Vulnerable, it is nevertheless listed as Near-threatened on account of its small range and dwindling numbers.

[*Aceros leucocephalus*,  
Mindanao, Philippines.  
Photo: Brian J. Coates]





The Sulu Hornbill was once found in large flocks on the southern Philippine islands of the Sulu Archipelago. The current situation is unclear, as the areas in question are of difficult access, but it seems that the species has disappeared from Jolo and is now extremely rare on Tawitawi, with perhaps only 20 pairs on the main mountain range of that island. Hunting, destruction of forest and collection of nestlings are major threats, and their influence continues unabated in the absence of control, while the activities of extremist political groups in the area make the prospect of conservation action slim. The Sulu Hornbill is perhaps the rarest member of the family and the closest to extinction.

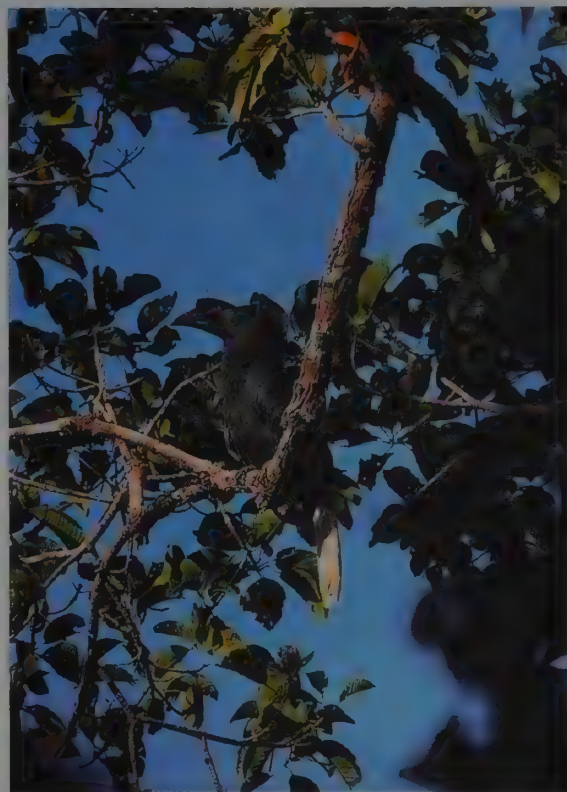
[*Anthracoceros montani*,  
Mt Sibangkat, Tawitawi,  
Sulu Archipelago,  
Philippines.  
Photo: Desmond Allen]

hornbills living in arid, sparsely timbered habitats in Namibia, where these artificial nest-sites are readily used and have greatly increased the density of breeding pairs. A few nestboxes provided in forest habitats have also been utilized successfully, but there is still considerable scope for developing practical artificial nesting sites for hornbills that feed in secondary forest. The modification and improvement of existing natural tree cavities is also a possibility, and has been successful with Southern Ground-hornbills in South Africa and with Great and Wreathed Hornbills in Thailand.

It should be emphasized that some frugivorous forest hornbills are responsible for the dispersal of the seeds of a significant proportion of economically important and ecologically dominant trees in African and Asian forests, so that for the viability of these forests, and the economic services they provide, the preservation of hornbills is almost certainly essential. For example, research has shown that some *Bycanistes* species were important dispersers of 56 of the 59 tree species on which they were recorded feeding. This constituted 22% of the tree flora in the forests which they inhabited. Even the smaller African Pied Hornbill was found to be a keystone species in the dispersal of seeds of trees along the forest edge and between small forest patches. The vital role of hornbills and other fruit-eating birds in seed dispersal and forest regeneration is set to increase as other, larger dispersers, especially mammals such as elephants, primates and squirrels, become rapidly rarer or are even eliminated from forest habitats. While this gives some hope that hornbill conservation will be taken seriously in at least a few regions, the same fact has provided little respite for frugivorous forest mammals and deserves wider publicity.

Methods and techniques for the study of wild hornbills in the field have expanded considerably. In Asia, these skills have been taught to researchers who attend courses, workshops and conferences run by the Hornbill Project Thailand, or who assist in projects organized by the Wildlife Conservation Society in Indonesia. Modern equipment has been developed for climbing forest trees and erecting hides, or blinds. Lights, mirrors and trapdoors designed for the examination of nest contents are now available. Precise locations of hornbills and their nests are recorded accurately by using satellite-linked Geographical Positioning Systems (GPS). Refinements in radio telemetry allow individual hornbills, when they are fitted with lightweight transmitters, to be tracked over long distances and for long periods, so that their daily and seasonal foraging needs can be gauged. Reliable methods of estimating hornbill numbers along forest trails, of assessing fruit crops of forest trees, and of determining tree structure and density within a study area are all now available. Forestry equipment for measuring the heights and sizes of trees and nests has been adopted, and a photographic technique to record details of nest entrances has been suitably modified. Moreover, the capturing of wild hornbills by using nets and drugs has been successfully pioneered, together with methods for marking individual birds that include the use of rings, tattoos and tags. These and other advances have considerably increased the knowledge and understanding of hornbill biology.

Obviously, any efforts, throughout the family's range, that will ameliorate the effects of habitat alteration or reduce the pressures on populations will be of positive value. One such is the creation of new conservation areas. In western India, attempts are being made to eliminate the lopping-off of fig branches to provide food for domesticated elephants, and to alter the practices used in honey-gathering so as to prevent damage to nest-cavities. In Thailand, programmes designed to inform the public and to encourage their involvement have been initiated on a wide scale. Local people, some of whom were previously poachers of hornbill nests, have been "converted" to nest guards in exchange for an annual stipend, which is provided by a "nest-adopter". In South Africa, the harvest of redundant second-hatched chicks of Southern Ground-hornbills that would normally die in the nest is being investigated, both as a sustainable resource for rural communities and as a source of birds for reintroduction. New surveys and field studies of hornbill biology, especially in India, Thailand, the Philippines, Indonesia, Cameroon, Namibia and South Africa, are providing important new information for conservation management.



The considerable part that the Bucerotidae play in the dispersal of seeds of forest trees is also being studied, especially in view of the decline in numbers of many larger mammal candidates for this ecological role.

Most importantly, the number of hornbill-observers, and of countries in which they study hornbills, rose considerably during the 1990's and is set to increase further. Many of these people are local residents, keen to influence their own politicians, countrymen and neighbours. In addition, regional zookeepers in North America, Europe and Africa have developed initiatives in captive management, including regional studbooks for some of the large hornbill species. Finally, an international Hornbill Specialist Group, with an annual newsletter, an Internet website and a list-server, helps to maintain contact among all those people interested in the appreciation, study and conservation of these magnificent birds.

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- Alexander *et al.* (1994), Ali (1976), Anderson (1876), Anggraini *et al.* (2000), Bartels & Bartels (1937), Bartlett (1869), Beddard (1889), Belterman & de Boer (1984), Benson (1968), Bigalke (1951), Bock (1994), Bock & Andors (1992), Bohmke (1988), Brouwer (1995), Burton (1984), Buttiker (1960), Camman (1950, 1951), Cotgreave (1999), Cracraft (1981, 1988), Crowe & Kemp (1988), Dierenfeld *et al.* (1991), Elliot (1877-1882), Ellison (1923), Feduccia (1999), Forshaw & Cooper (1994), Fraser (1981), Frith & Douglas (1978), Frith & Frith (1983b), Gould & Andau (1989), Hamman & Curio (1998), Harrison (1951), Harshman (1994), Hübner *et al.* (2000), Jain & Kannan (1967), Kemp (1970, 1976a, 1976b, 1979, 1988, 1994a, 1995a), Kemp & Crowe (1985), Kemp & Elbel (1988), Kemp & Grimes (1985), Korzun (1998), Leighton (1986), Liewviriyakit (1989), Lowe (1948), Mace (1994), Maurer (1978), Maurer & Raikow (1981), Mayr (1998), McMorris (1993), Moreau (1934, 1937), Moreau & Moreau (1940), Morin *et al.* (1994), Moynihan (1978), Ogilvie-Grant (1892), Pan Khangaun (1987a), Pang Bingzhang (1985), Peters (1945), Poonswad (1993a, 1998), Poonswad & Kemp (1993), Poonswad, Tsuji, Liewviriyakit & Jirawatkawi (1988a, 1988b), Reinhard & Blaszkiewicz (1986), Robiller & Trogisch (1985), Root & Root (1969), Sanft (1960), Shannon (1988), Sheppard (1988a, 1988b), Sibley (1996), Sibley & Ahlquist (1990), Sibley & Monroe (1990, 1993), Sibley *et al.* (1988), Steyn (1996b), Stresemann & Stresemann (1966), Tsuji (1996), Turner (1988), Verheyen (1955a, 1955b, 1955c), White, Kinney *et al.* (1984), Wilkinson (1992), Worth *et al.* (1994).



PLATE 35

## PLATE 35

## Family BUCEROTIDAE (HORNBILLS) SPECIES ACCOUNTS

### Subfamily BUCORVINAE

### Genus *BUCORVUS* Lesson, 1830

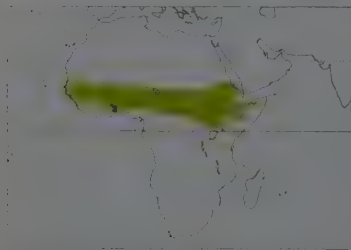
#### 1. Northern Ground-hornbill

##### *Bucorvus abyssinicus*

**French:** Bucorve d'Abyssinie **German:** Sudanhornrabe **Spanish:** Cálao Terrestre Norteño  
**Other common names:** Abyssinian Ground Hornbill

**Taxonomy.** *Buceros abyssinicus* Boddaert, 1783, Gondar, Ethiopia. Monotypic.

**Distribution.** S Mauritania and Guinea E to Ethiopia, NW Somalia, NE Kenya and Uganda.



**Descriptive notes.** 90-100 cm; male 4000 g. Very large hornbill with high casque, and yellow to orange patch at base of upper mandible; all black with white primaries. Male has bare facial skin blue and inflatable throat skin blue and red. Female similar to male, but with skin of face and throat all dark blue. Juvenile browner than adult, with black flecks in primaries; lacks casque, and has only a rather dull yellow patch on bill, and pale grey facial skin; reaches maturity after 3 years, but sex evident at 1 year.

**Habitat.** Inhabits savanna and sub-desert scrub, with variable grass cover, including

rocky and hilly areas; occurs at up to 3257 m in Ethiopia. Generally found in drier areas than is *B. leadbeateri*.

**Food and Feeding.** Eats wide variety of small vertebrates and invertebrates, including tortoises, lizards, spiders, beetles and caterpillars; also takes carrion, and some fruits, seeds and ground nuts. Forages in pairs, or with 1 or 2 offspring; mean group size c. 2-3, rarely, as many as 20 gather at abundant food. Walks slowly across ground in search of prey, which it catches with the bill.

**Breeding.** Little known in wild. Lays mainly in Jun-Aug in W Africa, from as early as Jan in Nigeria and Uganda, or as late as Nov in Kenya; captives in USA bred aseasonally. Nest in cavity in large tree, especially baobab (*Adansonia*) or palm stump, less often in rock hole or man-made bee-hive log or basket; male supplies most of deep lining of dry leaves; entrance not sealed. In captivity, normally lays 2 eggs at interval of c. 4-5 days; incubation 37-41 days, by female, fed at nest by male; chick c. 70 g at hatching, with pink skin that turns black within 10 days; fledging 80-90 days; female leaves chick and helps male with feeding from c. 21-33 days; second-hatched chick starves to death within c. 4 days, by which time older one may weigh 350 g. Captive pair lived for at least 40 years.

**Movements.** Adults apparently sedentary, but known to wander S in Kenya, then overlapping with *B. leadbeateri*. Juveniles apparently remain in parental home range for several years.

**Status and Conservation.** Not globally threatened. Widespread and common but sparse, with estimated home range of 260 km<sup>2</sup>, and more local in W Africa. Occurs in many reserves and at least 8 national parks. Protected as totem bird in some areas; but killed and mounted head used for hunting disguise in parts of Nigeria, Cameroon and Sudan, or chased locally as harbinger of bad luck in Gambia.

**Bibliography.** Anon. (1974, 1994b), Archer & Godman (1937-1961), Ash & Miskell (1998), Azua (1989), Balanço & de Visscher (1993), Bannerman (1953), Barlow *et al.* (1997), Beddard (1901), Britton (1980), Brown & Britton (1980), Cave & Macdonald (1955), Cawkell & Moreau (1963), Cheesman & Selater (1935), Cheke & Walsh (1996), Demey *et al.* (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Duckworth *et al.* (1992), Elgood *et al.* (1994), Fairfield (1973), Falzone (1988, 1989), Field (1999), Friedmann (1930a), Friedmann & Loveridge (1937), Fry *et al.* (1988), Garrod (1876), Giraudoux *et al.* (1988), Golding (1935), Gore (1990), Gregson (1994, 1996), Grimes (1987), Kemp (1994b), Kemp & Crowe (1985), Lamarche (1980, 1988), Lewis & Pomeroy (1989), Lippens & Wille (1976), Lipscomb (1938), Louette (1981b), Mace, M.E. (1987), Mackworth-Præd & Grant (1957, 1970), Morel & Morel (1990), Nikolaus (1987), Ottley (1879), Penny (1975), Rau (1986, 1988), Schratter (1997), Short *et al.* (1990), Smith (1957), Snow (1978), Toffie (1985), Waters (1984), Zimmerman *et al.* (1996).

#### 2. Southern Ground-hornbill

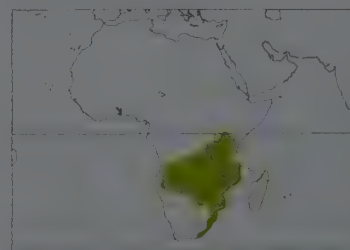
##### *Bucorvus leadbeateri*

**French:** Bucorve du Sud **German:** Kaffernhornrabe **Spanish:** Cálao Terrestre Sureño  
**Other common names:** Ground Hornbill, African Ground Hornbill

**Taxonomy.** *Buceros Leadbeateri* Vigors, 1825, Lower Bushman River, South Africa.

Species has often been listed as *B. cafer* on grounds that original description of *leadbeateri*, based on a specimen now lost, is claimed to refer to a female of *B. abyssinicus*; however, convincing evidence now suggests that the lost specimen was a female of present species, so *leadbeateri* should be retained and *cafer* considered a junior synonym. Monotypic.

**Distribution.** S Kenya and Burundi S to Angola, N Namibia, N & E Botswana, and NE & E South Africa.



**Descriptive notes.** 90-100 cm; male 3459-6180 g, female 2230-4580 g. Largest and heaviest hornbill species, all black with white primaries. Male has bare facial skin and inflatable throat skin bright red. Female differs in having blue patch on red throat skin. Juvenile browner than adult, with black flecks in primaries, grey sides to bill, and pale grey-brown facial skin; reaches maturity after 4-6 years, but in initial stages most closely resembles adult male.

**Habitat.** Inhabits woodland and savanna; also frequents grassland adjoining patches of forest, ranging up to 3000 m in l: African part of

range. Generally found in moister habitat than is *B. abyssinicus*.



**Food and Feeding.** Main diet made up of arthropods, such as grasshoppers, beetles, scorpions and termites; also, especially during dry season, insect larvae, snails, frogs and toads; sometimes larger prey, such as snakes, lizards, rats, hares, squirrels or tortoises. On occasion, feeds at carrion, taking scraps and associated insects. Fruits and seeds also recorded. Lives and hunts in groups of 2-8 members, rarely 11. Eats any small animals it can catch, and kills with pickaxe-like strikes from heavy bill. Digs in dung, ground or rotten wood. Larger prey often pursued and dismembered by several birds in the group.

**Breeding.** Lays mainly Sept-Dec. Co-operative breeder, dominant pair assisted by adult and immature helpers; defends territory. Nest in cavity, mainly in large tree or in rock face; male brings nest lining of dry leaves; entrance not sealed. Normally 2 eggs (85% of clutches), sometimes 1, rarely 3, laid at interval of 3-5 days or, rarely, up to 20 days; incubation 37-43 days, by dominant female, fed at nest by group-members; eggs hatch asynchronously, chick with pink skin that starts to turn black within 3 days; second-hatched chick starves to death within 1 week, rarely a month; chick fed c. 4-9 times daily by group-members, each carrying multiple items to nest in bill tip; fledges at c. 86 days, and remains with parental group at least until mature. One study in South Africa showed that a family group produced on average only 1 fledgling every 9 years.

**Movements.** Sedentary and territorial; no local movements described, except for dispersal at maturity, mainly by females.

**Status and Conservation.** Not globally threatened. Widespread and common, but sparse, with territories as small as 2-4 km<sup>2</sup> in N Zimbabwe, or up to 100 km<sup>2</sup> in NE South Africa. Occurs in

several reserves and at least seven national parks. Declines recorded in areas where increases occur in human density, tree-felling and use of poisoned baits, especially in South Africa and Zimbabwe, where group size and proportion of juveniles lowest outside protected areas; estimated 70% loss of range in South Africa. Also persecuted for breaking window panes by attacking own reflection in glass, and sometimes killed as superstitious token measure against drought. Protected by tribal lore in many areas, however, and able to co-exist with various forms of agriculture. Possibility of collecting second-hatched chicks for reintroduction programmes being investigated.

**Bibliography.** Ally & Butchart (2000), Anon. (1998c, 1998g), Beddard (1901), Benson & Benson (1977), Benson *et al.* (1971), Britton (1980), Brooke (1984), Brooke & Kemp (1973), Brown & Britton (1980), Browning (1992), Chiweshe (1994), Clancey (1996), Courtenay-Latimer (1942), Dean (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Ginn *et al.* (1989), Harrison *et al.* (1997), Hofer (1982), Jones (1969), Kemp, A.C. (1987, 1990, 1994b, 1995b, 1996, 1997), Kemp, A.C. & Begg (1996), Kemp, A.C. & Crowe (1985), Kemp, A.C. & Kemp (1975b, 1980, 1991), Kemp, A.C., Benn & Begg (1998), Kemp, A.C., Joubert & Kemp (1989), Kemp, M.I. & Kemp (1978), Knight (1990), Lewis & Pomeroy (1989), Lippens & Wille (1976), Lorber (1982), Macdonald (1984), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Magwizi (2000), Marais (1993, 1995), Mlingwa (1990), Nagai (2000), Penry (1994), Pinto (1983), Pithart *et al.* (1995), Ranger (1931), Runo & Davison (2000), Selater (1902), Seibt & Wickler (1977), Short *et al.* (1990), Simmons (1997), Snow (1978), Tramontana & Rider (1988), Vernon (1986), Waters (1984), Wickler & Seibt (1979), Zimmerman *et al.* (1996).





## Subfamily BUCEROTINAE

### Genus *ANORRHINUS* Reichenbach, 1849

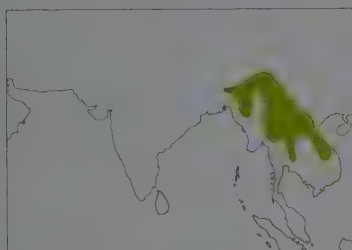
#### 3. Austen's Brown Hornbill

##### *Anorrhinus austeni*

**French:** Calao d'Austen **German:** Weißgesicht-Hornvogel **Spanish:** Calao Pardo de Austen  
**Other common names:** Assam/Brown(!)/White-throated Brown(-backed) Hornbill

**Taxonomy.** *Anorrhinus* [sic] *austeni* Jerdon, 1872, Asalu, Cachar Hills, Assam. Often separated with *A. tickelli* in genus *Ptilolaemus*; the two are often treated as conspecific, but differ in some plumage details and in presence or absence of sexual dimorphism in bill colour. Birds from Thailand and Indochina sometimes recognized as race *indochinensis*, but appear inseparable from other populations. Monotypic.

**Distribution.** NE India and S China to W, N & E Myanmar, N & C Thailand, Laos, W Cambodia and NW Vietnam.



**Descriptive notes.** 60–65 cm. Medium-sized hornbill, brown with white-tipped tail. Male has white cheeks and throat, pale creamy bill, rufous-brown underparts. Distinguished from *A. tickelli* by pale colour on head and throat. Female with head and throat all dark; generally more grey-brown below than male. Juvenile resembles adult male, with pale brown feather tips and dull yellow bare facial skin; sexual features evident from first moult, when c. 1 year old.

**Habitat.** Forest, both evergreen and deciduous, from lowland plains to edge of pine and oak forest in hills, but mainly in hill forest.

**Food and Feeding.** Fruit and small animals; diet includes 32 species of fruit, together with many arthropods, also bats, snakes, lizards, snails, earthworms, and chicks and eggs of other birds. In Thailand, when breeding, recorded food by weight 22% figs, 38% other fruits and 40% animals. Occurs as territorial groups of 2–15 birds, foraging together mainly in forest canopy, hawking, plucking and snatching food.

**Breeding.** Lays in India at start of rains, in Mar–Jun, and in Thailand at start of dry season, in Feb–Mar. Co-operative breeder, with dominant pair, male helpers and additional females. Nest mainly in natural cavity 32–40 cm wide or in old hole of Great Slaty Woodpecker (*Mulleripicus pulverulentus*), 5–18 m up in tall live forest tree, often *Dipterocarpus* or *Syzygium* species. Clutch 2–3 eggs, rarely up to 5; incubation 30 days; chick skin remains pinky yellow; female and chicks fed by all males in group, by regurgitation, mean rate c. 15 g per hour; fledging 62 days; female emerges with chicks at end of nesting cycle, after complete simultaneous moult of remiges and rectrices.

**Movements.** Apparently sedentary and territorial throughout range, except for local dispersal of young adults, yet flocks of 50 reported at times.

**Status and Conservation.** Not globally threatened. CITES II. Currently considered Near-threatened, even when lumped with *A. tickelli*. Only locally common, but has declined in many areas through loss of forest habitat, especially in E India, Thailand, S China, Laos and Vietnam. Eliminated from some areas, such as hills of NW Thailand and adjacent Myanmar, or populations isolated, as at Khao Yai National Park, in Thailand. Mean home range of breeding birds only 4.3 km<sup>2</sup>. Conservation status may merit reassessment, in light of taxonomic split.

**Bibliography.** Ali & Ripley (1983), Bangs & Van Tyne (1931), Chauliua *et al.* (1998), Cheng Tsohsin (1973), Deignan (1945), Duckworth *et al.* (1999), Frith & Douglas (1978), Ghosh (1994), Grimmett *et al.* (1998), Inskipp *et al.* (1996), Kemp (1988), Lan Yang & Xianji Wen (1993), Lekagul & Round (1991), MacKinnon & Philipps (2000), Ng Beechoo (1998), Poonswad (1993b, 1995), Poonswad & Tsuji (1994), Poonswad, Tsuji & Jirawatkavi (1991), Poonswad, Tsuji, Jirawatkavi & Chimchome (1998), Poonswad, Tsuji & Ngampongssai (1983, 1986, 1987, 1988), Ripley (1982), Robson (2000a), Robson *et al.* (1998), Smythies (1986), Stattersfield & Capper (2000), Stuart-Baker (1897), Thewlis *et al.* (1998), Tikader (1983), Tsuji *et al.* (1987), Worth *et al.* (1994), Zhao Zhengjie (1995).

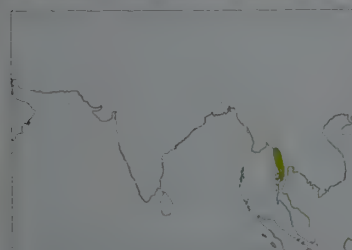
#### 4. Tickell's Brown Hornbill

##### *Anorrhinus tickelli*

**French:** Calao brun **German:** Rostbauch-Hornvogel **Spanish:** Calao Pardo de Tickell  
**Other common names:** Brown(!)/Brown-backed/Rusty-cheeked Hornbill

**Taxonomy.** *Buceros Tickelli* Blyth, 1855, Tenasserim, Myanmar. Often separated with *A. austeni* in genus *Ptilolaemus*; the two are often considered conspecific, but differ in some features of plumage and in presence or absence of sexual dimorphism in bill colour. Monotypic.

**Distribution.** S Myanmar (Tenasserim) and adjacent W Thailand.



**Descriptive notes.** 60–65 cm; male 854–912 g, female 683–797 g. Medium-sized hornbill, red-brown below, darker brown above. Male has brighter rufous cheeks and throat, pale yellow bill. Distinguished from *A. austeni* by brown throat. Female darker below, with dusky brown bill; distinguished from female *A. austeni* by dark bill. Juvenile of both sexes resembles adult male, but paler brown.

**Habitat.** Evergreen and deciduous hill forest, especially areas of taller and denser trees; from foothills to 1500 m.

**Food and Feeding.** Not recorded; probably similar to that of *A. austeni*.

**Breeding.** Laying recorded during Feb–Apr in Myanmar. Breeds co-operatively, in groups. Nest in natural cavity in tree at 3.5–8 m. Of 8–10 adults present at one nest, at least 5 males brought food.

**Movements.** Probably sedentary and territorial, but recorded as irregular visitor to higher forest.

**Status and Conservation.** Not globally threatened. CITES II. Currently considered Near-threatened, even when lumped with *A. austeni*. Has smallest range of any continental hornbill species. Habitat loss to logging and agriculture known to be prevalent within its range. Surveys and studies of biology urgently needed. Conservation status probably merits reassessment, in light of taxonomic split.

**Bibliography.** Baker (1934a), Bingham (1879), Forshaw & Cooper (1994), Inskipp *et al.* (1996), Kekule (1999), Kemp (1988), Lekagul & Round (1991), Ng Beechoo (1998), Poonswad (1993b), Poonswad, Chimchome *et al.* (1998), Robson (2000a), Round (1985), Smythies (1986), Stattersfield & Capper (2000), Tickell (1864), Worth *et al.* (1994).

#### 5. Bushy-crested Hornbill

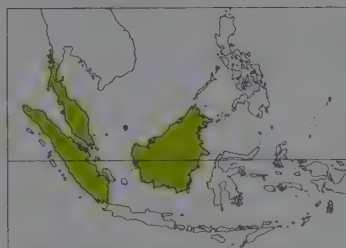
##### *Anorrhinus galeritus*

**French:** Calao largup **German:** Kurzschopf-Hornvogel **Spanish:** Calao Crestado  
**Other common names:** Buffy-crested Hornbill

**Taxonomy.** *Buceros galeritus* Temminck, 1831, Pontianak, Borneo.

Has been considered distinct from congeners and thus treated as sole member of genus, with *A. austeni* and *A. tickelli* then placed in *Ptilolaemus*. Birds from S Myanmar and Malay Peninsula sometimes separated as race *carinatus* and those from Borneo as *minor*, but neither seems sufficiently distinct. Monotypic.

**Distribution.** Extreme S Myanmar and S Thailand S through Peninsular Malaysia to Sumatra, and N Natuna Is and Borneo.



**Descriptive notes.** 65–70 cm; 1134–1247 g. Medium-sized, dark brown hornbill with green sheen on back, and grey-brown tail with broad black end. Male has black bill. Female differs in having mostly yellowish bill, with black around base, extending variably along cutting edges. Juvenile resembles adult male, but with brown tips to feathers, bill pale olive-green, eyes brown, bare facial skin pale yellow; acquires adult colours during second year.

**Habitat.** Evergreen forest, at up to 1800 m. Favours dense foothill forest with high densities of fig trees, at up to c. 750 m, but can survive and breed in selectively logged forest.

**Food and Feeding.** Fruits; also cicadas and other insects, and lizards and frogs. Takes lipid-rich fruits, with at least 30 species recorded, mainly Meliaceae and Myristicaceae; also figs, which represent 10% of diet. Forages in groups of 6–10 individuals, rarely up to 20, feeding mainly below the canopy during short visits to trees. Group also joins in chasing off competitors, including other hornbill species, at fruiting trees. Bouts of hunting animals for c. 25% of time, digging among foliage, bark and capsules, or group-members combining in pursuit of agile prey. Group may split up when food in short supply.

**Breeding.** Lays at various times of year, when food abundant; sometimes breeds twice yearly or only once in 2 years. Co-operative, with whole group perching together to call in territorial display and helping at nest; only dominant pair breeds, and helpers mainly males. Nest in natural tree cavity at 10–25 m. Clutch 2–3 eggs; incubation c. 30 days; chick retains dull pink skin; female moults remiges and rectrices simultaneously; female and chicks fed by whole group, mainly by regurgitation; fledging c. 60 days; female emerges c. 1 week before chicks fledge; juveniles remain with parental group for at least 5 months.

**Movements.** Sedentary and territorial, with no reports of movements other than dispersal of immatures.

**Status and Conservation.** Not globally threatened. CITES II. Widespread, but only locally common, at densities as high as 1.2 km<sup>2</sup>/per group. In Sumatra, occurs in Way Kambas National Park and in Kerinci-Seblat National Park. Eliminated from areas of intensive logging, so range reduced, especially in lowland areas. Ability to survive in secondarily logged dipterocarp forest and areas with smaller trees suggests some resilience to habitat alteration.

**Bibliography.** Anggraini *et al.* (2000), Buri (1996), Danielsen & Heegaard (1995), Davison (1995), Frith & Douglas (1978), Holmes (1996), Holmes *et al.* (1993), Jeyarajasingam & Pearson (1999), Johns (1987, 1988), Kemp (1988), Leighton (1982, 1986), Leighton & Leighton (1983), Lekagul & Round (1991), MacKinnon & Philipps (1993), Madge (1969), van Marle & Voous (1988), Medway & Wells (1976), Nash & Nash (1985, 1988), Ng Beechoo (1998), Poonswad (1993b), Riley (1938), Robson (2000a), Round (1985, 1988), Smythies (1986, 1999), Vowles & Vowles (1984), Walton & Watt (1987), Wells (1985, 1999), Wilkinson, Dutson & Sheldon (1991).

### Genus *TOCKUS* Lesson, 1830

#### 6. Crowned Hornbill

##### *Tockus alboterminatus*

**French:** Calao couronné **German:** Kronentoko **Spanish:** Toco Coronado  
**Other common names:** African Crowned Hornbill

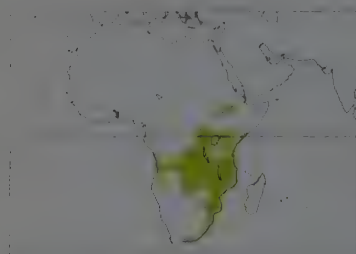
**Taxonomy.** *Lophoceros alboterminatus* Büttikofer, 1889, Gambos, Angola.

Forms a superspecies with *T. bradfieldi* and *T. fasciatus*; closely related also to *T. hemprichii*, all four having similar calls and displays. Various races proposed on basis of differences in size and darkness of plumage, including *geloensis* from NE & E of range, *suahelicus* from E coastal forest, *stegmanni* from Uganda to E Zaire and W Tanzania, *angolensis* from N Angola and nearby parts of Zaire, and *australis* from S, but populations intergrade widely. Species formerly referred to as *Lophoceros melanoleucos*, but this name clearly applies to some other taxon, possibly *Anthraceroceros albirostris*. Monotypic.

**Distribution.** SW Ethiopia; NE Zaire, NW Uganda, C Kenya and S Somalia S to Angola, extreme NE Namibia, Zimbabwe, Mozambique and E South Africa.

**Descriptive notes.** 50 cm; male 191–332 g, female 180–249 g. Small, sooty-brown hornbill with broad white eyebrow, white belly and white tip to tail. Male has darkish orange-red bill with fairly





obvious casque, orange eye, and yellow-orange line at base of bill. Distinguished from *T. bradfieldi* by darker plumage, darker bill with larger casque. Female differs from male in smaller casque, yellow eye, yellow basal bill line, green throat skin. Juvenile with white flecks on wing-coverts, yellow bill, bare dull yellow throat skin.

**Habitat.** Montane, riverine and coastal forest, and stands of tall dense woodland and secondary forest. At times, enters gardens in built-up areas.

**Food and Feeding.** Diet mainly arthropods and fruit, the latter especially during dry season; also snails, nest contents of small birds, lizards, and golden moles (*Chrysochloris*). Wide variety of insects, including distasteful grasshoppers and hairy caterpillars; also at least 20 types of fruit, including crops such as oil palm (*Elaeis guineensis*), peanuts, maize and bananas. Forages mainly among canopy foliage, often plucking off insects, or hawking them on the wing.

**Breeding.** Lays in Oct-Jan, at start of rainy season, in C & S Africa; less seasonal in E Africa, in Feb-Jul or Sept-Nov. Territorial in pairs. Nest in natural cavity, 1-2-12 m up in tree trunk or large branch; male brings lining mostly of bark flakes, female seals nest entrance mainly with own droppings. Clutch 2-5 eggs, after pre-laying period of 7-14 days; incubation 25-27 days, by female, starting from first egg, so chicks hatch 2-4 days apart; chick with pink skin throughout; female moults remiges and rectrices simultaneously, regrown by emergence 25-30 days after hatching of oldest chick; male feeds female and chicks at nest, assisted latterly by female; fledging 46-55 days; juveniles remain in family party until following season.

**Movements.** Sedentary in more stable evergreen forest, but forms flocks of up to 80 and wanders far from breeding territory in more deciduous habitats or during drought. Regular altitudinal and local movements in parts of E Africa, more erratic and irregular in S.

**Status and Conservation.** Not globally threatened. Widespread and locally common in suitable habitat. Densities vary greatly, from 1 pair/7 ha to 1 pair/500 ha. Ability to wander at times of food shortage allows occupation of marginal habitats and response to local disturbance; even enters cities and gardens if necessary. Occurs in numerous national parks, e.g. Shimba Hills (Kenya), Lake Manyara (Tanzania), South Luangwa (Zambia) and Lengwe (Malawi). Numbers only locally reduced through cutting of forest and woodland, as in Somalia.

**Bibliography.** Anon. (1998b), Ash & Miskell (1998), Aspinwall (1986), Benson & Benson (1977), Benson *et al.* (1971), Britton (1980), Brown & Britton (1980), Claassen (1992), Clancey (1996), Colgreave (1999), Dean (1973, 2000), Dowsett (1990), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Evans & Anderson (1992), Fry *et al.* (1988), Gardner (1998), Ginn *et al.* (1989), Grant & Mackworth-Præd (1946), Harrison *et al.* (1997), Irwin (1982), Kemp (1976a), Kemp & Crowe (1985), Leonard (1998b), Lewis & Pomeroy (1989), van der Linde (1992), Lippens & Wille (1976), Macdonald (1984), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Moreau (1935), Nikolaus (1987), Pinto (1983), du Plessis (1994a, 1995), Prigogine (1980), Ranger (1941, 1949-1952), Riddell (2000), Short *et al.* (1990), Siemens (1981), Snow (1978), Urban, E.K. & Brown (1971), Urban, M. & Caraviotis (1996), Vernon (1988), Zimmerman (1972), Zimmerman *et al.* (1996).

## 7. Bradfield's Hornbill

### *Tockus bradfieldi*

**French:** Calao de Bradfield

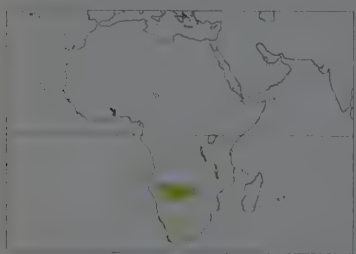
**German:** Felsentoko

**Spanish:** Toco de Bradfield

**Taxonomy.** *Rhynchoceros bradfieldi* Roberts, 1930, Waterberg, Namibia.

Forms a superspecies with *T. alboterminatus* and *T. fasciatus*; closely related also to *T. hemprichii*, the four all having similar calls and displays. In past, birds of N Botswana and W Zimbabwe sometimes separated in race *willaminae*. Monotypic.

**Distribution.** S & SE Angola, NE Namibia, SW Zambia, N Botswana and W Zimbabwe.



**Descriptive notes.** 50 cm; 180-395 g. Small, pale brown hornbill with white belly and white tip of tail. Male has whitish stripe behind eye, orange bill with yellow band across base, small casque. Distinguished from *T. alboterminatus* by paler plumage and bill, smaller casque. Female somewhat smaller, with less distinct stripe behind eye, smaller casque. Juvenile with smaller, paler bill.

**Habitat.** Deciduous *Baikiaea* and *Pterocarpus* woodland on sandy soils, and adjacent stands of tall mopane (*Colophospermum*) woodland; wanders in nomadic fashion to wide range of neighbouring habitats, from grassy or woody

savanna to riverine forest.

**Food and Feeding.** Diet mainly arthropods, especially beetles and termites, augmented by various seeds during May-Aug dry season; in wet season, also frogs, lizards and fruit. Forages mainly among foliage and along branches, often on the wing, but during dry winter months regularly hops about on ground and digs, especially in animal dung, in search of food.

**Breeding.** Lays at start of wet season, in Sept-Dec; second attempts Mar. Nest in natural cavity in tree or rock face, once 7 m up, and always with escape chimney; male delivers bark lining, female seals entrance at least 10 days before starting to lay. Clutch 3 eggs; incubation uncertain, but at least 38 days from sealing in to hatching; female moults remiges and rectrices simultaneously, but emerges 32 days through nestling period to assist male in delivering food to nest; male delivers single items in bill, collected 1 m to at least 2 km away from nest; fledging at least 48 days.

**Movements.** Sedentary and territorial when breeding. During dry season, forms loose flocks of up to 70 birds which wander locally in search of food.

**Status and Conservation.** Not globally threatened. Only locally common, and with patchy distribution. Possibly resilient to changes in habitat through ability to wander in search of food and nest-sites. Affected locally where woodland is damaged by humans or elephants, with recent 40% range loss in Zimbabwe, but exists in several large conservation areas. Occurs in Chobe National Park, in Botswana, Waterberg Plateau National Park, in Namibia, and Hwange National Park, in Zimbabwe. Total range, however, although spanning 5 countries, is among the smallest for any continental hornbill species.

**Bibliography.** Anon. (1998b), Benson (1982), Benson *et al.* (1971), Borello & Borello (1994), Brown (1993), Chadwick (1984), Dean (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Ginn *et al.* (1989), Harrison *et al.* (1997), Herremans & Herremans-Tonneoyr (1994c), Hines (1996),

Hoesch (1937), Hustler (1993), Hustler & Mitchell (1996), Irwin (1982), Kemp (1976a), Kemp & Crowe (1985), Mackworth-Præd & Grant (1962), Maclean (1993), Meyer de Schauensee (1932), Newman (1996), Penry (1987, 1994), Pinto (1983), Snow (1978).

## 8. African Pied Hornbill

### *Tockus fasciatus*

**French:** Calao longibande

**German:** Elstertoko

**Spanish:** Toco Blanquenegro

**Other common names:** Allied/Pied(1)/Zande Hornbill, Black-and-white-tailed Hornbill

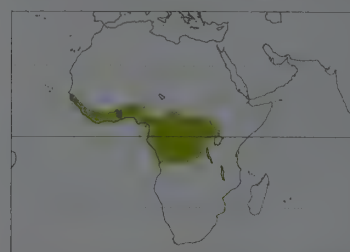
**Taxonomy.** *Buceros fasciatus* Shaw, 1811, Malimbe, Angola.

Forms a superspecies with *T. alboterminatus* and *T. bradfieldi*; closely related also to *T. hemprichii*, all having similar calls and displays. Two subspecies recognized.

**Subspecies and Distribution.**

*T. f. semifasciatus* (Hartlaub, 1855) - Senegambia E to SW Nigeria.

*T. f. fasciatus* (Shaw, 1811) - SE Nigeria to S Chad and E to Uganda, S to N Angola and SC Zaire.



**Descriptive notes.** 50 cm; male 250-316 g, female 191-260 g. Small, glossy black hornbill with white belly. Male nominate race has white outer tail feathers; bill pale yellow with dark red at tip and extending back as lines along casque and cutting edges; bare skin around eye and small bare throat patch dark blue. Female smaller, bill with smaller casque and black, not red, markings, throat patch orange. Juvenile with small, pale yellow bill, no obvious casque, only tips of outer tail feathers white. Race *semifasciatus* slightly smaller than nominate, only tips of outer tail feathers white, bill markings black in both sexes and more extensive.

**Habitat.** Lowland evergreen forest and adjacent patches of secondary forest, also gallery forest, dense deciduous woodland and, more recently, oil palm (*Elaeis guineensis*) plantations and open farmland mosaic, at up to 900 m.

**Food and Feeding.** Diet mainly insects and fruit, in about equal proportions by number; also takes some spiders, and small vertebrates such as tree-frogs, lizards, mice, bats, and nest contents of small birds. Recorded to eat variety of fruits from at least 14 plant genera, including oil palms. Forages mainly in or above the foliage, at all levels. Mainly hawks insects on or above the canopy, at 30-50 m, but will descend lower and even take food from ground. Fruit digested for period of over an hour, but seeds voided unharmed for germination. Congregates at sources such as fruiting oil palms, often roosting communally.

**Breeding.** Little known. Lays generally in drier months, Aug in Senegal, Sept-Apr in Liberia, Nov-Apr in rest of W Africa, Sept-Feb in Gabon, Mar-Apr and Sept in Uganda, and Jul-Sept in Zaire. Nest 9-38 m up in natural cavity in tree, highest in primary forest; entrance sealed by female, using own droppings. Largest recorded clutch 4 eggs; female fed at nest by male at rate of 6-12 items per hour, usually moults remiges and rectrices simultaneously, but emerges before chicks to help male with food delivery. A captive survived at least 22 years.

**Movements.** Sedentary and probably territorial over much of range. Forms into flocks of up to 70 in non-breeding season, especially in drier and more marginal habitats, and these wander widely in search of food.

**Status and Conservation.** Not globally threatened. Widespread, and locally common to very common. One of few hornbill species of lowland forest to adapt readily to secondary and even tertiary forest habitats, so has gained as well as lost habitat in many areas. Ability to forage above vegetation and to range widely in search of food also enhances adaptability. Plays key role in dispersal of tree seeds between forest and adjacent habitats.

**Bibliography.** Bannerman (1953), Barlow *et al.* (1997), Britton (1980), Brosset & Énard (1986), Brown & Britton (1980), Cave & Macdonald (1955), Chapin (1939), Cheke & Walsh (1996), Christy & Clarke (1994), Colston & Curry-Lindahl (1986), Dean (2000), Dowsett & Dowsett-Lemaire (1991, 1993, 1997), Dowsett & Forbes-Watson (1993), Dutton & Branscombe (1990), Elgood *et al.* (1994), Field (1999), Fry *et al.* (1988), Gartshore (1989), Gartshore *et al.* (1995), Gatter (1997), Germain *et al.* (1973), Gore (1990), Grimes (1987), Jenseth (1995), Jenseth & Eilenberg (1997, 1999), Kemp (1976a), Kemp & Crowe (1985), Lippens & Wille (1976), Louette (1981b), Mackworth-Præd & Grant (1957, 1962, 1970), Morel & Morel (1990), Nikolaus (1987), Pinto (1983), Prigogine (1980), Rand (1951), Sauvage & Rodwell (1998), Serle (1957), Short *et al.* (1990), Snow (1978), Thiollay (1970), Thomas (1991), Voisin (1953), Young (1946).

## 9. Hemprich's Hornbill

### *Tockus hemprichii*

**French:** Calao de Hemprich

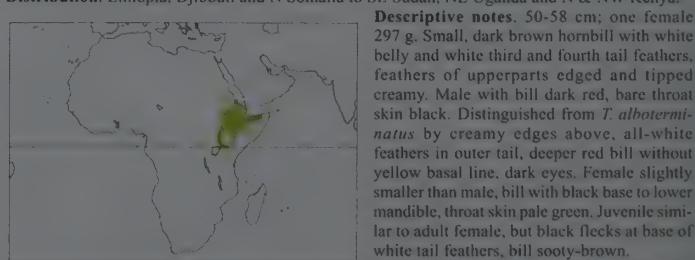
**German:** Hemprichtoko

**Spanish:** Toco Abisinio

**Taxonomy.** *Buceros (Lophoceros) Hemprichii* Ehrenberg, 1833, Archiko, Ethiopia.

Most closely related to superspecies formed by *T. alboterminatus*, *T. bradfieldi* and *T. fasciatus*, having similar whistling calls and head-up display posture with wings closed. In past, birds of N Kenya occasionally separated as race *exsul*. Monotypic.

**Distribution.** Ethiopia, Djibouti and N Somalia to SE Sudan, NE Uganda and N & NW Kenya.



**Descriptive notes.** 50-58 cm; one female 297 g. Small, dark brown hornbill with white belly and white third and fourth tail feathers, feathers of upperparts edged and tipped creamy. Male with bill dark red, bare throat skin black. Distinguished from *T. alboterminatus* by creamy edges above, all-white feathers in outer tail, deeper red bill without yellow basal line, dark eyes. Female slightly smaller than male, bill with black base to lower mandible, throat skin pale green. Juvenile similar to adult female, but black flecks at base of white tail feathers, bill sooty-brown.

**Habitat.** Occupies wooded watercourses in

hilly areas and along gorges, at up to 4300 m in Ethiopian Highlands.

**Food and Feeding.** Eats mainly insects, but also lizards and chameleons, and some fruits, figs and berries. Forages by moving in buoyant flight from tree to tree. Takes most food from among the



foliage, or by hawking flying insects; also descends to ground to feed on termites, or to search among rock cracks.

**Breeding.** Little known. Lays mainly in Mar-May, also in Aug-Oct and Jan in Ethiopia. Territorial display ends with unique fanning of tail over back. Nest most often in natural hole in rock face on side of ravine, sometimes in tree cavity, even in hole in wall of old building; lined with flakes of wood and bark; nest sealed by female. Clutch 3 eggs; incubation by female, fed at nest by male with single items carried in bill; incubation and fledging periods undocumented.

**Movements.** Apparently resident over most of range; in peripheral areas of Eritrea, Somalia and Kenya, however, descends into flat lowlands, forms into small flocks of up to 14, and wanders far from normal breeding habitat.

**Status and Conservation.** Not globally threatened. Widespread and common in Ethiopia, but local and often uncommon elsewhere. Favoured habitat often remote and inaccessible, which reduces extent of habitat alteration and human interference. Occurs in Forêt du Day National Park, in Djibouti.

**Bibliography.** Archer & Godman (1937-1961), Ash & Miskell (1998), Bennun & Njoroge (1996, 1999), Britton (1980), Brown (1976), Cave & Macdonald (1955), Cheesman & Selater (1935), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Duckworth *et al.* (1992), Friedmann (1930a), Fry *et al.* (1988), Harvey (1998a, 1998b), Hegner (1980), Kemp (1976a), Kemp & Crowe (1985), Lewis & Pomeroy (1989), Mackworth-Præd & Grant (1957), Short *et al.* (1990), Smith (1957), Snow (1978), Urban & Brown (1971), Urban *et al.* (1970), Williams (1978), Zimmerman *et al.* (1996).

## 10. Pale-billed Hornbill

### *Tockus pallidirostris*

**French:** Calao à bec pâle

**German:** Blaßschnabeltoko

**Spanish:** Toco Piquiclaro

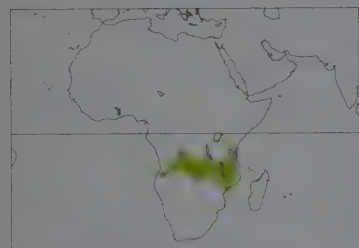
**Taxonomy.** *Buceros pallidirostris* Hartlaub & Finsch, 1870, Caconda, Angola.

Forms a superspecies with *T. nasutus*. Races occasionally hybridize at W edge of Luangwa Valley, in Zambia. Two subspecies recognized.

**Subspecies and Distribution.**

*T. p. pallidirostris* (Hartlaub & Finsch, 1870) - EC, C & NE Angola, S Zaire, and E Zambia (W of Luangwa Valley).

*T. p. neumanni* (Reichenow, 1894) - Zambia (E from Luangwa Valley), Malawi, SE Tanzania and N Mozambique.



**Descriptive notes.** 43-50 cm; male 248-325 g, female 170-217 g. Small hornbill, pale grey and brown above, upperparts edged buffish, with white stripe behind eye and white tip to tail, white below. Male of nominate race has bill pale yellow with greyish tip, fairly low casque. Female smaller, with browner eye; casque ridge smaller. Juvenile with small, casqueless bill. Race *neumanni* smaller than nominate, head paler; bill shows grey blotching, tip red.

**Habitat.** Extensive stands of tall, dense deciduous miombo (*Brachystegia*) woodland. Where range overlaps with that of *T. nasutus*, occurs in denser, less open woodland.

**Food and Feeding.** Few details available. Probably mainly insectivorous, but known to eat seeds and gum from damaged pods. Forages mainly among foliage; sometimes descends to ground for food, mainly in dry season.

**Breeding.** Little known. Lays at start of rainy season, in Aug-Nov, even before many trees in leaf. Nest in natural cavity in tree, entrance sealed to a narrow slit. Clutch 4-5 eggs, laying interval unrecorded; incubation by female, fed at nest by male; chicks staggered in size; female moults flight-feathers and tail feathers simultaneously; incubation and fledging periods not documented.

**Movements.** None reported, but may move locally during dry season when trees drop their leaves. Race *neumanni* recorded as vagrant in S Kenya.

**Status and Conservation.** Not globally threatened. Widespread and locally common. Large areas of habitat still exist, some of it in large reserves; occurs in Mikumi National Park, in Tanzania. Many areas, however, especially in Malawi and more populated areas of Zambia and Mozambique, have been opened up, allowing colonization by *T. nasutus* at expense of present species

**Bibliography.** Anon. (1993), Aspinwall & Beel (1998), Benson & Benson (1977), Benson *et al.* (1971), Britton (1980), Dean (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Johnston-Stewart & Heigham (1982), Kemp (1976a), Kemp & Crowe (1985), Lippens & Wille (1976), Mackworth-Præd & Grant (1957, 1970), Msowoya (1996), Newman *et al.* (1992), Pinto (1983), Roberts (1912), Short *et al.* (1990), Snow (1978), Ulfstrand & Alerstam (1977).

## 11. African Grey Hornbill

### *Tockus nasutus*

**French:** Calao à bec noir

**German:** Grautoko

**Spanish:** Toco Piquinegro

**Other common names:** Grey Hornbill(!)

**Taxonomy.** *Buceros nasutus* Linnaeus, 1766, Dakar, Senegal.

Forms a superspecies with *T. pallidirostris*. Larger, darker birds from NE Ethiopia and SW Arabia described as race *forskali*, and paler ones from S Angola and Namibia as *dorsalis*, but neither now seems distinct enough to warrant recognition. Two subspecies currently recognized.

**Subspecies and Distribution.**

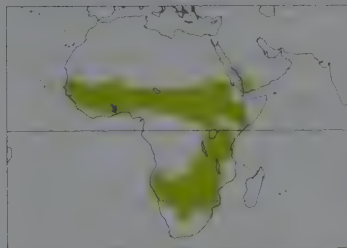
*T. n. nasutus* (Linnaeus, 1766) - S Mauritania E to Ethiopia and W Somalia, S to N Sierra Leone, N Uganda and N Kenya; SW Saudi Arabia and W Yemen.

*T. n. ephraim* (Sundevall, 1851) - S Uganda and S Kenya S to C Namibia and N South Africa.

**Descriptive notes.** 45-51 cm; male 172-258 g, female 163-215 g. Small, dark grey and brown hornbill, wing feathers pale-edged, with white stripe behind eye, white back, white tip to tail and white belly. Male nominate race has black bill with white at base of upper mandible, white ridges at base of lower. Distinguished from *T. pallidirostris* by white on back, darker bill with smaller casque. Female smaller than male, bill and casque cream, bill tip maroon. Juvenile resembles adult male, but bill smaller with no casque. Race *ephraim* smaller, male with distal protrusion of casque, female with ridges on lower mandible less distinct.

**Habitat.** Open savanna and deciduous woodland, from margins of sub-desert and grassland to edges of dense woodland and forest.

**Food and Feeding.** Mainly insects, especially arboreal grasshoppers, beetles, mantids and scale insects (Coccidae); also tree-frogs, chameleons, lizards, and nest contents of small birds: some fruit



months. Territorial in pairs. Nest in natural cavity in tree at 0.7-9 m, in rock face, or in old hole of barbet in tree or ground, lined with bark flakes and few dry leaves; same site often used in successive years. Clutch 2-5 eggs, after pre-laying enclosure 5-11 days; incubation 24-26 days; chick hatches with pink skin, which retained; male feeds female and chicks with single food items delivered in bill tip; female moults remiges and rectrices simultaneously, but emerges when oldest chick 19-34 days old to assist male in brood-feeding; sometimes, male feeds at nest of other hornbill species; fledging 43-49 days.

**Movements.** Sedentary in areas with mixed deciduous woodland and evergreen riparian trees; elsewhere, often forms loose flocks and ranges widely in dry season, when trees lose leaves. Flocks of 50-100 make regular N-S movements to remain in leafy habitat across sub-Saharan W & NE Africa, moving N in May-Jun and S in Oct-Nov; rare vagrant to Liberia; movements more erratic and variable in E & S Africa, especially in drought years, when extends to S limits of range.

**Status and Conservation.** Not globally threatened. Widespread and common both in Africa and in Arabia, occupying wide range of habitats and capable of extensive movements in search of food. Common in many large reserves, and also moves into suburban areas.

**Bibliography.** Ash & Miskell (1983, 1998), Bannerman (1953), Barlow *et al.* (1997), Benson & Benson (1977), Benson *et al.* (1971), Boix-Hinzen (1997), Britton (1980), Brooke (1956), Brooks *et al.* (1987), Brown (1940), Brown & Britton (1980), Cave & Macdonald (1955), Cheesman & Selater (1935), Cheke & Walsh (1996), Cornwallis & Porter (1982), Cotgreave (1999), Cunningham-van Someren (1977b), Dean (2000), Diop & Tréca (1997), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Duckworth *et al.* (1992), Elgood, Fry & Dowsett (1973), Elgood, Heigham *et al.* (1994), Evans, M.I. (1994), Field (1999), Fitz-Gerald (1997), Friedmann (1930a), Fry *et al.* (1988), Gatter (1997), Ginn *et al.* (1989), Giraudeau *et al.* (1988), Gore (1981, 1990), Grimes (1987), Harrison *et al.* (1997), Jennings (1995), Kemp (1973, 1976a), Kemp & Crowe (1985), Kemp & Kemp (1972), Lack (1985), Lewis (1984a), Lewis & Pomeroy (1989), Lippens & Wille (1976), Mace (1992), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Mendelsohn (1997), van der Merwe (1991), Newby (1980), Nuttall (1992), Penry (1994), Phillips (1982), Pinto (1983), Porter *et al.* (1996), Rahmani *et al.* (1994), Rands *et al.* (1987), Rieker (1988), Robel (1997), Ryall (1984), Short *et al.* (1990), Snow (1978), de Swardt *et al.* (1992), Tarboton *et al.* (1987), Tree (1963a, 1979), Wilkinson & McLeod (1991), Zimmerman *et al.* (1996).

## 12. Monteiro's Hornbill

### *Tockus monteiri*

**French:** Calao de Monteiro

**German:** Monteirotoko

**Spanish:** Toco Angoleño

**Taxonomy.** *Toccus* [sic] *monteiri* Hartlaub, 1865, Benguela, Angola.

Considered closest to *T. erythrorhynchus*, but also close to *T. leucomelas*, *T. flavirostris* and *T. deckeni*, based on similar calls and behaviour, and DNA studies. In past, S populations occasionally separated as race *marjoriae*. Monotypic.

**Distribution.** SW Angola and NW & C Namibia.



**Descriptive notes.** 50 cm; male 370 g, female 269-423 g. Small hornbill, dark grey, brown and white, with pale stripe behind eye, white-spotted wing-coverts, and outer tail feathers all white apart from brown base. Male with notably large, dark red bill, dark grey bare throat skin. Female with somewhat smaller bill, turquoise throat skin. Juvenile with smaller, pale orange bill with dark brown patch at base.

**Habitat.** Dry scrub and open thornbush savanna, mainly among stony hills or on adjacent flats.

**Food and Feeding.** Eats mainly insects, of wide variety, especially grasshoppers and large,

spiny crickets; also, some fruits, seeds, flowers and underground bulbs. Forages mainly on ground, hopping from rock to rock, or digging hard and deep with the heavy bill.

**Breeding.** Lays Oct-Mar, c. 1 month after first good fall of rain, but mostly in Jan-Mar. Territorial in pairs. Nest usually in natural cavity in rock face, or in large tree along watercourse, lined with leaves, bark and grass; readily uses artificial nestboxes; female seals entrance with own droppings and food remains, although male brings some mud and millipedes to assist; crushed millipedes secrete antibiotic, which probably helps in nest hygiene. Clutch 2-8 eggs, following pre-laying period 5-11 days; incubation 24-27 days; eggs hatch at intervals of 2-4 days, chick with pink skin, which retained; male delivers food to female and chicks, up to 3 items at once carried in bill tip; female moults remiges and rectrices simultaneously at time of laying, but emerges when oldest chick 19-25 days old to feed herself and help feed chicks; fledging 43-46 days. Clutch size and breeding success variable between years, depending on rainfall; mean brood size at fledging 1.5-2.8 young.

**Movements.** Sedentary in some areas of higher rainfall, but rains generally unpredictable. During dry season, often forms flocks (up to 47 birds recorded in a flock) which wander in search of food, even into flat, sandy areas.

**Status and Conservation.** Not globally threatened. Generally common and widespread within limited range. Occurs mainly in inhospitable areas of low human population density, including a few large reserves, e.g. Waterberg Plateau National Park (Namibia). Also in Namibia, since 1980 has adapted to use nestboxes extensively in Daan Viljoen Reserve.

**Bibliography.** Boix-Hinzen (1998a, 2000), Boix-Hinzen *et al.* (2000), Brown (1993), Dean (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Ginn *et al.* (1989), Harrison *et al.* (1997), Kemp (1973, 1976a), Kemp & Crowe (1985), Kemp & Kemp (1972), Klaassen (1996), Klaassen & Brenninkmeijer (1997), Mackworth-Præd & Grant (1962), Maclean (1993), Mendelsohn (1997), Newman (1996), Pinto (1983), Rieker (1988), Sinclair & Sinclair (1995), Snow (1978), Stanback *et al.* (1998).





### 13. Red-billed Hornbill

#### *Tockus erythrorhynchus*

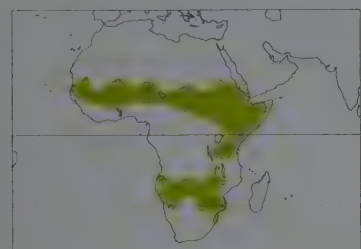
**French:** Calao à bec rouge **German:** Rotschnabeltoko **Spanish:** Toco Piquirrojo  
**Other common names:** African Red-billed Hornbill; South African Red-billed Hornbill (*rufostris*); Damaraland Red-billed Hornbill (*damarensis*)

**Taxonomy.** *Buceros erythrorhynchus* Temminck, 1823, Podor, Senegal.

Closest to *T. monteiri*, but also close to *T. leucomelas*, *T. flavirostris* and *T. deckeni*, based on similar calls and behaviour, and DNA studies. Races *rufostris* and *damarensis* may be two separate species. Population from S Mozambique to Natal described as race *degens* on basis of smaller size, but differences slight; birds of N Botswana (Ngamiland) formerly separated as race *ngamiensis*. Yellow-eyed birds from Tanzania, with black circumorbital skin, may represent as yet undescribed race, as also may birds in N Kenya; further study needed. Four subspecies currently recognized.

**Subspecies and Distribution.**

*T. e. kemp* Tréca & Éard, 2000 - S Mauritania and Senegambia E to Inner Niger Delta.  
*T. e. erythrorhynchus* (Temminck, 1823) - Inner Niger Delta E to Ethiopia and Somalia, S to Tanzania.  
*T. e. rufostris* (Sundevall, 1851) - S Angola and N Namibia E to Zambia and S Malawi and S to NE South Africa.  
*T. e. damarensis* (Shelley, 1888) - NW & C Namibia.



**Descriptive notes.** 35 cm; male 124-220 g, female 90-200 g. Small, black and white hornbill with spotted wing-coverts, white in outer tail, and long, slender, red bill. Male nominate race has thin yellow basal line of bill, black inner half of lower mandible; bare skin around eye and on throat yellow to pinkish; eyes brown. Female smaller, lower mandible with only small black patch. Juvenile resembles adult male, but bill shorter and pale orange. Races differ mainly in size, eye colour, and colour of facial skin and feathering: *kemp* smaller, with black facial skin; *rufostris* slightly larger than nominate, darker grey on

face to upper breast, less black on bill, facial skin flesh-coloured, eyes yellow; *damarensis* larger still, head to breast whiter, facial skin dark fleshy, bill and eyes as nominate.

**Habitat.** Open savanna and woodland, especially with sparse ground cover, extending into drier thorn-scrub and more hilly areas in Namibia and sub-Saharan areas; occurs at up to 2100 m in Ethiopia.

**Food and Feeding.** Beetles, termites, fly larvae and grasshoppers important in diet, but takes small vertebrates such as geckos, nestlings and rodents when these available; some fruit eaten, and in dry season even grain, especially by nominate race. Most food obtained on ground, particularly by digging in dung and debris for small insects. Often joins bird parties. Nominative race forages more often in trees, especially when competitive congeners are absent.

**Breeding.** Lays usually 4-7 weeks after start of rains: Mar-Nov in W Africa, various months in NE & E Africa, Apr-May in Somalia, Feb-Mar in Namibia, and Sept-Feb in C & S Africa. Territorial in pairs. Nest in natural cavity 0.3-9.1 m up in tree, in old hole of barbet or woodpecker, or in bee-hive log, lined with green leaves and some bark and dry grass; male selects site, and sometimes brings lining and sealing materials to assist, female seals entrance with own droppings and food remains; often takes over nest of other hornbill species, once when still containing chicks. Clutch 2-7 eggs, laid 1-7 days apart following pre-laying period 3-24 days; incubation 23-25 days, starting from first egg; female and chicks fed by male; female moults remiges and rectrices simultaneously during laying, but emerges when oldest chick 16-24 days old; fledging 39-50 days.

**Movements.** In some areas, congregates during dry season in flocks of several hundred, which make local movements in search of food; this is evident in Zambezi Valley of Zimbabwe and, especially, arid sub-Saharan zones, where it may amount to regular migration. Unusual drowning of c. 1000 birds in L Kariba, in Zimbabwe, apparently on migration.

**Status and Conservation.** Not globally threatened. A widespread and locally common species, with many populations in large reserves. If some discrete races or populations prove to be full species, as in W & SW Africa, their smaller ranges may make them more vulnerable. Generally benefits from sparse ground cover created by stocking with game or livestock, provided sufficient trees suitable for nesting remain. In Namibia, race *damarensis* regularly uses artificial nestboxes.

**Bibliography.** Anon. (1998), Archer & Godman (1937-1961), Ash & Miskell (1983, 1998), Bannerman (1953), Barlow *et al.* (1997), Benson & Benson (1977), Benson *et al.* (1971), Britton (1980), Brown & Britton (1980), Cave & Macdonald (1955), Cheesman & Selater (1935), Cheke & Walsh (1996), Clancey (1964b), Coborn (1978), Cotgreave (1999), Dean (2000), Delpont (1999), Diop (1993), Diop & Tréca (1993, 1995, 1997), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Elgood *et al.* (1994), Elliott (1972), Eneke (1970), Friedmann (1930a), Fry *et al.* (1988), Ginn *et al.* (1989), Giraudoux *et al.* (1988), Gore (1990), Grimes (1987), Harrison *et al.* (1997), Keen (1997), Kemp (1973, 1976a), Kemp & Crowe (1985), Lack (1985), Lewis & Pomeroy (1989), Mackworth-Præd & Grant (1957, 1962, 1970), Maclean (1993), Mendelsohn (1997), Moreau (1938), Neunzig (1930), Penry (1994), Pinto (1983), Reinhard & Strehlow (1998), Rickert (1988), Roots (1968), de Ruiter (1993a), Runo (2000), Scheres & Alba (1997), Schifter (1986), Short *et al.* (1990), Simmons (1979a), Smith (1957), Snow (1978), Tarboton *et al.* (1987), Tréca & Éard (2000), Wambuguh (1987, 1988), von Wiesche (1928), Zimmerman *et al.* (1996).

### 14. Southern Yellow-billed Hornbill

#### *Tockus leucomelas*

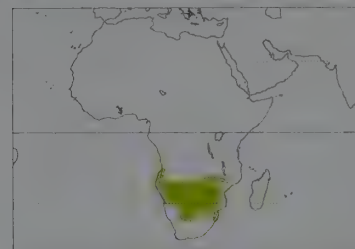
**French:** Calao leucomèle **German:** Südlicher Gelbschnabeltoko **Spanish:** Toco Piquigualdo Sureño

**Taxonomy.** *Buceros leucomelas* M. H. K. Lichtenstein, 1842, Vaal River, South Africa.

Sometimes considered to form a superspecies with *T. flavirostris* and in the past treated as conspecific, but differs in voice and bare-part colours. These two closely related to *T. deckeni*, and also, more distantly, to *T. monteiri* and *T. erythrorhynchus*, based on similar calls and behaviour, and DNA

studies. Birds from Angola described as race *elegans*, on basis of smaller size, paler plumage and differences in bare-part colours, and those from E of range as *parvior*, on basis of smaller size, but degree of variation in all populations uncertain; further study needed. Monotypic.

**Distribution.** SW Angola and Namibia E to S Malawi, W Mozambique and N South Africa.



**Descriptive notes.** 40 cm; male 153-242 g, female 138-211 g. Small, black and white hornbill with spotted wing-coverts, white in outer tail, and long yellow bill with only slight casque. Male with casque extending to tip of bill; bare skin around eye and on throat dark fleshy; eyes yellow, possibly occasionally brown. Distinguished from *T. flavirostris* by colour of circumorbital and throat skin. Female smaller, with shorter casque. Juvenile with dark brown blotches on short dull yellow bill, grey eyes.

**Habitat.** Scattered trees along watercourses in semi-desert in W, throughout open savanna and woodland in E.

**Food and Feeding.** Diet mainly arthropods, especially termites, ants, beetles, caterpillars and grasshoppers, but also centipedes, scorpions, solifugids; some rodents taken, mainly during plagues, and bird eggs; also some fruit and seeds. Forages mainly on ground, picking off small animals and fruit from surrounding vegetation and ground litter; digs only infrequently, but turns over debris or chases prey when necessary.

**Breeding.** Lays after first summer rains, in Sept-Mar; rarely, second brood. Territorial in pairs. Nest in natural cavity 0.8-12.2 m up in tree; male brings lining of grass, leaves and bark; female seals entrance with own droppings and sticky food remains, sometimes assisted by male with lumps of mud. Clutch 2-6 eggs, preceded by pre-laying enclosure 4-5 days; incubation 24 days; chick hatches with and retains pink skin; female and chicks fed by male; female moults remiges and rectrices at same time, but emerges when oldest chick 19-27 days old, chicks reveal nest and then fed by male and female; fledging 42-47 days. Preyed on by wide range of raptors and small mammals.

**Movements.** Local seasonal movements reported from lowveld to escarpment of South Africa, and in more arid Kalahari, but occur most often during droughts.

**Status and Conservation.** Not globally threatened. Widespread and common in most parts of range, at densities of c. 1 pair/20 ha. Remains in areas with various forms of farming, and eliminated only where nest trees are removed. Common in several extensive protected areas.

**Bibliography.** Benson & Benson (1977), Benson *et al.* (1971), Boix-Hinzen (1997), Brown (1993), Clancey (1959b, 1996), Dean (1973, 2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Fry *et al.* (1988), Ginn *et al.* (1989), Harrison *et al.* (1997), Herholdt & De Villiers (1989), Heston (1983), Hines (1990, 1996), Kemp (1973, 1976a), Kemp & Crowe (1985), Macdonald (1984), Mackworth-Præd & Grant (1962), Marshall (1984), Mendelsohn (1997), Newman (1996), Parker (1999), Penry (1994), Pinto (1983), Prozesky (1965), Sharp (1986), Sinclair & Sinclair (1995), Tarboton *et al.* (1987).

### 15. Eastern Yellow-billed Hornbill

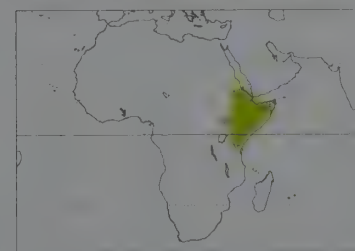
#### *Tockus flavirostris*

**French:** Calao à bec jaune **German:** Östlicher Gelbschnabeltoko **Spanish:** Toco Piquigualdo Norteño  
**Other common names:** Yellow-billed Hornbill

**Taxonomy.** *Buceros flavirostris* Rüppell, 1835, Taranta Mountains, Ethiopia.

Sometimes considered to form a superspecies with *T. leucomelas*, and in past usually treated as conspecific, but differs in voice and bare-part colours. These two closely related to *T. deckeni*, and also, more distantly, to *T. monteiri* and *T. erythrorhynchus*, based on similar calls and behaviour, and DNA studies. Slightly smaller birds from NE Somalia described as race *somaliensis*, mainly on basis of orange markings on bill, but this character apparently variable; further research required. Monotypic.

**Distribution.** Ethiopia, Djibouti and Somalia S to SE Sudan, NE Uganda, Kenya and NE Tanzania.



**Descriptive notes.** 40 cm; male 225-275 g, female 170-191 g. Small, black and white hornbill with spotted wing-coverts, white in outer tail, and large orange-yellow bill with only slight casque. Male with casque extending to tip of bill; bare skin around eye black; throat skin extensive, pink, inflated when breeding; eyes yellow. Distinguished from *T. leucomelas* by colours of facial and throat skin. Female smaller, casque smaller, throat skin black. Juvenile with small, dull yellow bill with brown patches.

**Habitat.** Open thornbush savanna and *Commiphora* woodland.

**Food and Feeding.** Orthopterans and termites common in diet, together with some figs, and fruits of *Commiphora* and *Boscia*. Forages mainly on ground, and simply picks up most food items, but feeds regularly in trees to take fruit. Mutualistic association with dwarf mongooses (*Helogale undulata*), feeding on flushed insects, especially locusts, in exchange for predator surveillance. May drink regularly when water available.

**Breeding.** Little known. Lays in Feb-Mar in Kenya, in Mar-May (possibly Oct-Nov) in Ethiopia and Somalia. Territorial in pairs, with head-down open-winged display. Nest in natural cavity 1.5-4.5 m up in tree or rock face, lined with bark and wood chips. Clutch 2-3 eggs; female fed in nest by male with single items carried in bill tip, moults remiges and rectrices together at start of laying; incubation and fledging periods not documented.

**Movements.** Sedentary in most areas, but suggested to move out of Somali lowlands into adjacent foothills during dry season.

**Status and Conservation.** Not globally threatened. Generally uncommon, but wide range includes several large reserves and areas with low human densities. Vulnerable to cutting-down of nest trees in such open habitats.



**Bibliography.** Archer & Godman (1937-1961), Ash & Miskell (1983, 1998), Bennun & Njoroge (1999), Britton (1980), Brown & Britton (1980), Cave & Macdonald (1955), Cotgreave (1999), Cunningham-van Someren (1986), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Friedmann (1930a), Fry *et al.* (1988), Kemp (1973, 1976a), Kemp & Crowe (1985), Lack (1985), Lewis & Pomeroy (1989), Mackworth-Præd & Grant (1957), Nikolaus (1987), North (1942), Rasa (1981, 1983), Richards (1995), Short *et al.* (1990), Smith (1957), Urban & Brown (1971), Zimmerman *et al.* (1996).

## 16. Von der Decken's Hornbill

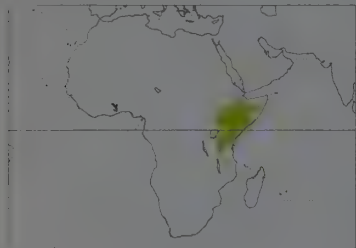
### *Tockus deckeni*

**French:** Calao de Decken **German:** Von-der-Decken-Toko **Spanish:** Toco Kenia  
**Other common names:** Decken's Hornbill; Jackson's Hornbill (*jacksoni*)

**Taxonomy.** *Buceros (Rhynchaceros) Deckeni* Cabanis, 1869, Seyidie Province, Kenya. Closest to *T. leucomelas* and *T. flavirostris*, but also close to *T. monteiri* and *T. erythrorhynchus*, based on similar calls and behaviour, and DNA studies. Race *jacksoni* distinctive, often considered a separate species. Two subspecies recognized.

#### Subspecies and Distribution.

*T. d. deckeni* (Cabanis, 1869) - Ethiopia, S Somalia, Kenya (except NW) and Tanzania.  
*T. d. jacksoni* (Ogilvie-Grant, 1891) - SE Sudan, NE Uganda and NW Kenya.



**Descriptive notes.** 35 cm; male 165-212 g, female 120-155 g. Small, pied hornbill with white back and wing patches and white in outer tail feathers. Male nominate race with black wings and wing-coverts, apart from white middle secondaries and middle greater coverts; bill with low casque to tip, red with yellow outer half, black cutting edges; eye patch and bare skin around eye black; throat skin fleshy; eyes brown. Female smaller, bill and casque smaller and black. Juvenile with spotted wing-coverts, small dark horn bill with yellow patches. Race *jacksoni* smaller, spotting on wing-coverts at all ages, adult male with less yellow on bill.

**Habitat.** Open savanna and woodland, especially with *Commiphora* and thorn trees.

**Food and Feeding.** Mainly small animals, with some fruits, seeds and buds. Insects important in diet, also snails, mice, birds, lizards and frogs. Forages mainly on ground, or drops down from perch on to prey, but feeds relatively high up in fruiting trees. Special mutualistic relationship with dwarf mongooses (*Helogale undulata*), eating flushed insects and offering warning against common predators.

**Breeding.** Lays in Feb-Jul in N of range, in Nov-Mar farther S. Territorial in pairs. Nest in natural cavity 0.5-5 m up in tree, palm stump, old woodpecker hole, or even in cliff, lined with bark flakes. Clutch 2-4 eggs, laid at intervals of up to 5 days; incubation c. 30 days; female fed by male with single items carried in bill tip, moults remiges and rectrices at start of laying, but emerges to help feed brood when oldest chick 21-28 days old; fledging 47-50 days.

**Movements.** Sedentary, and no movements reported, but may wander locally during periods of drought. **Status and Conservation.** Not globally threatened. Widespread and locally common; large populations in a number of large reserves and national parks, and in areas with low human density. Vulnerable only in areas where nest trees have been cut down.

**Bibliography.** Ash & Miskell (1983, 1998), Bennun & Njoroge (1996, 1999), Britton (1980), Brown & Britton (1980), Cave & Macdonald (1955), Cotgreave (1999), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Duckworth *et al.* (1992), Ellis (1976, 1993a, 1993b), Friedmann (1930a), Fry *et al.* (1988), Kemp (1976a), Kemp & Crowe (1985), Lack (1985), Lewis & Pomeroy (1989), Mackworth-Præd & Grant (1957), Moreau (1935), Nikolaus (1987), Paterson (1992), Rasa (1981, 1983), Richards (1995), Sanft (1954), Short *et al.* (1990), Urban & Brown (1971), Williams (1978), Zimmerman *et al.* (1996).

## 17. Black Dwarf-hornbill

### *Tockus hartlaubi*

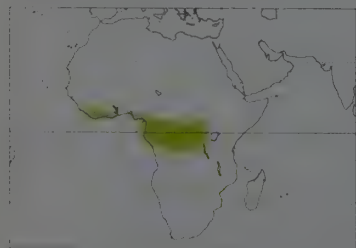
**French:** Calao de Hartlaub **German:** Hartlaubtoko **Spanish:** Toco Negro  
**Other common names:** Dwarf Black Hornbill

**Taxonomy.** *Toccus* [sic] *hartlaubi* Gould, 1861, Fanti, Ghana.

Two subspecies recognized.

#### Subspecies and Distribution.

*T. h. hartlaubi* Gould, 1861 - S Sierra Leone and S Guinea E to S Cameroon and SW Central African Republic, and S to Gabon and N Congo.  
*T. h. granti* (Hartert, 1895) - EC Congo and Zaire (Congo Basin) E to S Sudan and W Uganda, and S to NW Angola (Cabinda).



**Descriptive notes.** 32 cm; male 96-135 g, female 83-99 g. Small, mostly black hornbill with broad white eyestripe, white tip to tail and dark bill. Male of nominate race has casque reaching to approximately half-way along bill, red tip to bill; bare skin around eye blackish; throat skin flesh-coloured; eyes reddish-brown, rims grey. Female smaller than male, casque smaller, bill without red. Juvenile similar to adult female. Race *granti* has white tips to wing-coverts, red casque.

**Habitat.** Inhabits higher subcanopy areas of tall evergreen and gallery forest, especially where lianas and other small-diameter

perches present; only rarely in secondary forest.

**Food and Feeding.** Mainly insects, especially larger beetles and grasshoppers, but also smaller ones such as caterpillars; also large spiders, small lizards; rarely, fruit. Feeds mainly at 20-45 m, making frequent sallies to pick prey from foliage, often from underside of leaves. Also hawks insects in flight, and often hovers briefly. Sometimes follows troops of monkeys or, at ground level, driver-ants, taking insects disturbed by them.

**Breeding.** Little known. Lays aseasonally, in Feb, Jun or mainly Oct-Dec, in W Africa; in Jun-Dec in C Africa. Apparently territorial, in pairs. Nest in natural cavity 9-35 m up in branch or trunk; female seals herself in. Probably up to 4 eggs; female fed by male with single items carried in bill

tip, emerges before chicks fledge to help male; incubation and fledging periods not documented; broods of 1-3 recorded.

**Movements.** Probably sedentary and territorial throughout year.

**Status and Conservation.** Not globally threatened. Secretive and relatively quiet, but probably locally common. Small size and spatial requirements of c. 20-30 ha/pair ensure reasonable densities. Occurs in several reserve areas, including Gola Forests Reserve in Sierra Leone and Tai Forest National Park in Ivory Coast, but restricted to pristine forest, which makes it vulnerable to any forest alteration.

**Bibliography.** Bannerman (1953), Berlioz & Roché (1960), Britton (1980), Brosset & Énard (1986), Chapin (1939), Cheke & Walsh (1996), Christy & Clarke (1994), Colston & Curry-Lindahl (1986), Dean (2000), Dowsett & Dowsett-Lemaire (1991, 1993, 1997), Dowsett & Forbes-Watson (1993), Dutton & Branscombe (1990), Elgood *et al.* (1994), Farmer (1979), Field (1999), Friedmann (1966), Fry *et al.* (1988), Gartshore (1989), Gartshore *et al.* (1995), Gatter (1997), Germain *et al.* (1973), Green & Carroll (1991), Grimes (1987), Helsen (1996), Kemp (1976a), Kemp & Crowe (1985), Lippens & Wille (1976), Louette (1981b), Mackworth-Præd & Grant (1957, 1970), Nikolaus (1987), Pinto (1983), Sargeant (1993), Snow (1978), van Someren (1949), Thomas (1991).

## 18. Red-billed Dwarf-hornbill

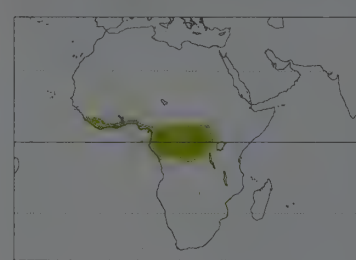
### *Tockus camurus*

**French:** Calao pygmée **German:** Zwergtoko **Spanish:** Toco Pardo  
**Other common names:** Dwarf (Red-billed) Hornbill

**Taxonomy.** *Tockus camurus* Cassin, 1857, Cape Lopez, Gabon.

In past, birds from Nigeria westwards sometimes separated as race *pulchrirostris*. Monotypic.

**Distribution.** S Sierra Leone and S Guinea E to W Uganda, S to NW Angola (Cabinda) and S Zaire.



**Descriptive notes.** 30 cm; male 101-122 g, female 84-115 g. Smallest hornbill, with distinctive chestnut colour, white-spotted wing-coverts, white edges to flight-feathers, white belly. Male with bill all bright red, bare skin around eye brown, eyes white to pale yellow. Female smaller, bill with black tip. Juvenile with smaller bill pale orange, eyes grey.

**Habitat.** Dense understorey of primary, secondary and gallery forest, including around swamps, forest margins and in small patches, at up to 800 m.

**Food and Feeding.** Insects, mainly small ants, wasps and mantids, also larger grasshoppers;

lizards also recorded; only rarely fruit. Forages in groups of up to 6 birds, occasionally 12, at lower levels of forest, usually below 20 m and down to forest floor. Gleans from small branches and foliage; agile, climbs branches in flattened posture. Often follows squirrels and driver-ants for the insects they disturb. Readily joins bird parties, when very vocal.

**Breeding.** Little known. Lays in Feb-Sept and Nov-Dec in W Africa, in Oct-Dec in C Africa. In groups of up to 12 birds that often call together throughout year, so probably breeds co-operatively. Captive pair called and displayed together, bouncing up and down with wings spread. Nest in natural cavity in tree, once 14 m up with entrance hole sealed to narrow slit. Clutch size and incubation period unknown; chick with pink skin retained throughout; female emerges to help male about half-way through nestling period; in captivity, total nesting cycle 81 days, 2 chicks fledged.

**Movements.** Probably sedentary and territorial throughout year.

**Status and Conservation.** Not globally threatened. Widespread and commonly heard; one group in forest patch of c. 20 ha in Gabon; elsewhere, about every 800 m along 32 km of riverine forest. Easily overlooked in dense growth. Tolerates wide range of forest conditions, including secondary forest, so less affected than most other hornbill species by habitat alteration. Occurs in several large reserves. Further data required on breeding biology.

**Bibliography.** Bannerman (1953), Bates (1930), Bouet (1961), Brosset & Énard (1986), Cave & Macdonald (1955), Chapin (1939), Christy & Clarke (1994), Claffey (1999), Colston & Curry-Lindahl (1986), Dean (2000), Dowsett & Dowsett-Lemaire (1991, 1993, 1997), Dowsett & Forbes-Watson (1993), Dutton & Branscombe (1990), Elgood *et al.* (1994), Field (1999), Fry *et al.* (1988), Gartshore (1989), Gartshore *et al.* (1995), Gatter (1997), Germain *et al.* (1973), Green & Carroll (1991), Grimes (1987), Kemp (1976a), Kemp & Crowe (1985), Lippens & Wille (1976), Louette (1981b), Mackworth-Præd & Grant (1957, 1970), Maclachy (1937), Martin (1982), Nikolaus (1987), Pinto (1983), Sargeant (1993), Serie (1957), Snow (1978), van Someren (1949), Thiollay (1976), Thomas (1991).

## Genus *TROPICRANUS* W. L. Sclater, 1922

## 19. Long-tailed Hornbill

### *Tropicranus albocristatus*

**French:** Calao à huppe blanche **German:** Weißschopf-Hornvogel **Spanish:** Cálao Crestiblanco  
**Other common names:** Crowned(!)/White-crowned(!)/White-crested Hornbill

**Taxonomy.** *Buceros albo-cristatus* Cassin, 1848, St Paul's River, Liberia.

Often placed in genus *Tockus*, or occasionally in *Berenicornis*, but appears to be sufficiently distinct in behaviour and voice, as well as in some aspects of morphology, to merit treatment in monospecific genus. Three subspecies recognized.

#### Subspecies and Distribution.

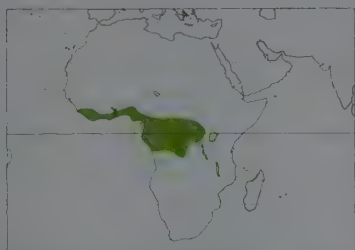
*T. a. albocristatus* (Cassin, 1848) - S Sierra Leone, S Guinea, Liberia and W Ivory Coast.

*T. a. macrourus* (Bonaparte, 1850) - E Ivory Coast to Benin.

*T. a. cassini* (Finsch, 1903) - Nigeria E to W Uganda, S to N Angola.

**Descriptive notes.** 70 cm; male 279-315 g, female 276-288 g. Elongate, black hornbill with bushy white crest, and very long, graduated tail with white tip. Male nominate race with face, crown and nape feathers white with black tips, body all black; bill with casque ending near tip, blackish, upper mandible with large cream patch at base; skin around eye blue, throat skin flesh-coloured, eyes yellow. Female smaller, casque ridge shorter. Juvenile with small greenish bill, no casque initially, eyes bluish. Race *macrourus* similar to nominate, but has white extending to neck; *cassini* larger,





sides of head black, not white, greater coverts, primaries and tertiaries tipped white, little or no cream on bill.

**Habitat.** Dense tangles within stands of primary forest, but extends to tall gallery and secondary forest, even to adjacent deciduous woodland; occurs at up to 1500 m.

**Food and Feeding.** Mainly insects, but also spiders, slugs, lizards, snakes, shrews and nestlings; frequently eats fruit, some of which taken from ground. Forages mainly 5-30 m up amid dimly lit understorey, picking food off foliage, lianas and small stems; sometimes swoops to ground after prey. Often follows troops of monkeys, driver-ants or bird parties to hawk insects disturbed by them.

**Breeding.** Little known. Lays aseasonally, in Jan-Feb, Apr and Aug-Nov in W Africa, and in Jan-Feb, Jun-Aug and Oct-Dec in C Africa. Territorial in pairs, territory preferably shared with a monkey troop. Nest in natural cavity 10-16 m up in tree or palm stump; female seals entrance with own droppings. Clutch 2 eggs; female moults remiges and rectrices together when breeding; male carries insects to nest singly in bill tip; incubation and fledging periods not recorded.

**Movements.** Probably sedentary and territorial in most areas.

**Status and Conservation.** Not globally threatened. Widespread and locally common, but patchily distributed in W of range; generally absent from Dahomey Gap, though present in suitable areas of forest, e.g. locally not uncommon in Togo; estimated density of 3-4 pairs/km<sup>2</sup> reported for Zwedru and Glaro (Liberia). Secretive, and often in dense shaded foliage, thus avoiding detection. Tolerates wide range of forest types, and occurs in several large reserves. Commonest where monkey troops present, but remains common even when monkeys eliminated. Data required on breeding biology.

**Bibliography.** Bates (1930), Brosset & Dragesco (1967), Brosset & Éard (1986), Chapin (1939), Cheke & Walsh (1996), Christy & Clarke (1994), Colston & Curry-Lindahl (1986), Dean (2000), Dowsett & Dowsett-Lemaire (1991, 1993, 1997), Dowsett & Forbes-Watson (1993), Dutton & Branscombe (1990), Elgood *et al.* (1994), Field (1999), Fry *et al.* (1988), Gartshore (1989), Gartshore *et al.* (1995), Gatter (1997), Germain *et al.* (1973), Green & Carroll (1991), Grimes (1987), Halleux (1994), Helsens (1996), Kemp (1976a), Kemp & Crowe (1985), Lippens & Wille (1976), Louette (1981b), Mackworth-Praed & Grant (1957, 1970), MacLachy (1937), Pinto (1983), Rand (1951), Sergeant (1993), Serle (1957), Snow (1978), van Someren (1949), Thomas (1991), Wild (1996), Willis (1983).

## Genus *OCYCEROS* Hume, 1873

### 20. Malabar Grey Hornbill

*Ocyrceros griseus*

**French:** Calao gris

**German:** Malabartoko

**Spanish:** Cálao Gris Malabar

**Taxonomy.** *Buceros griseus* Latham, 1790, Bombay, India.

Genus sometimes combined with African *Tockus*, but differs in feeding behaviour at nest. Sometimes considered to form a superspecies with *O. gingalensis*, or the two often treated as conspecific, but they differ in bare-part colours and some morphological and behavioural details. Monotypic.

**Distribution.** Western Ghats of SW India.



**Descriptive notes.** 45 cm; male 238-340 g. Small hornbill with grey, black and white plumage, broad pale eyebrow stripe, rufous vent, and bill with oval nostrils. Male with bill and low casque orange-yellow, bill tip paler; skin around eye and on throat black; eyes red-brown. Distinguished from *O. gingalensis* by somewhat paler plumage, more prominent eyebrow, grey breast, rusty vent, more orangey bill, black circumorbital skin, oval nostrils. Female smaller than male, bill paler yellow, blackish patches on smaller casque, black at base of lower mandible. Juvenile like adult female, but with buff edges to wing-coverts, smaller paler bill.

**Habitat.** Evergreen and deciduous forest, especially along watercourses and in hill country above 600 m, but extends to lowlands and also enters gardens and plantations.

**Food and Feeding.** Mainly fruit and berries, particularly figs; also insects and lizards; rarely, flowers. One study of male feeding female (and latterly young) imprisoned in nest revealed that lipid-rich fruits predominated (37%), followed by figs (26%), other sugar-rich fruits (23%) and animal items (14%); delivery frequency of animal foods increased after hatching. Forages in groups, with up to 20 gathering at fruiting trees.

**Breeding.** Lays in Jan-May, at end of dry season. Possible courtship display involves forward bows. Nest in cavity in live, usually large forest tree, at average height of 16.5 m; 80% of cavities are holes produced by natural rot, rest excavated by other birds; entrance diameter c. 8 cm, mean tree diameter at cavity 42 cm; one cavity was 25 cm wide, 36 cm deep, with 63-cm chimney above; female alone seals cavity. Clutch 2-4 eggs; female moults remiges and rectrices simultaneously; male delivers fruit to nest in throat, but may carry insect in bill tip; multiple items regurgitated one by one; in one study, 2397 items delivered by male during period of incarceration; incubation c. 40 days; fledging c. 46 days; female and young emerge from nest together. In studies of 27 nests, chicks fledged at 89%.

**Movements.** Apparently sedentary; may move locally in more deciduous habitats.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in Western Ghats EBA. Reported to be declining in N part of range, and generally vulnerable to clearing of forest throughout Western Ghats. Still locally common, including in some small reserves, but less widespread than previously. Occurs in Periyar National Park, and Indira Gandhi and Perambikulam Wildlife Sanctuaries.

**Bibliography.** Abdulali (1942, 1951), Ali (1935-1937, 1996), Ali & Ripley (1983), Baker (1934a, 1934b), Daniels (1997), Gaston & Zacharias (1996), Gokula & Vijayan (1997), Grimmer *et al.* (1998), Inskipp *et al.* (1996), Kannan (1998), Kazmierczak (2000), Kemp (1976a, 1988), Mahabal & Lamba (1987), Mudappa (1994, 1995,

1997, 1998, 2000a, 2000b), Mudappa & Kannan (1997), Neelakantan (1976), Poonswad (1993b), Ripley (1982), Saha & Dasgupta (1992), Stattersfield *et al.* (1998), Sugathan & Varghese (1996), Zacharias & Gaston (1999).

### 21. Sri Lankan Grey Hornbill

*Ocyrceros gingalensis*

**French:** Calao de Ceylan

**German:** Ceylontoko

**Spanish:** Cálao Gris Cingalés

**Taxonomy.** *Buceros Gingalensis* Shaw, 1811, Colombo, Sri Lanka.

Genus sometimes combined with African *Tockus*, but separated by differences in feeding behaviour at nest. Sometimes considered to form a superspecies with *O. griseus*, or the two often treated as conspecific, but differences in bare-part colours and in some aspects of behaviour and morphology suggest better treated as separate species. Monotypic.

**Distribution.** Sri Lanka.



**Descriptive notes.** 45 cm; male 238 g. Small grey hornbill with thin pale streaks on head, white tips to primaries and white outer tail; circular nostrils. Male has creamy bill with dusky base; bare circumorbital and throat skin dark purple, eyes red. Female smaller, bill black with yellowish streak. Juvenile with pale greenish bill.

**Habitat.** Evergreen forest and deciduous woodland, especially areas with dense creepers; also found in plantations and large gardens. Occurs at up to 1200 m.

**Food and Feeding.** Mainly fruit, especially small figs, but also variety of wild and cultivated species; also insects, frogs, lizards, scorpions. Forages mainly among foliage below canopy, often perching for long periods on lookout for food. May gather in small groups at fruiting trees.

**Breeding.** Little known. Lays in Mar-Jul, peak May, but sometimes lays as late as Oct. Nest in natural cavity 2-21 m up in tree, or in old hole of woodpecker. Clutch 1-3 eggs; incubation 28-30 days; female moults remiges and rectrices together while breeding; male delivers food in throat and regurgitates at nest, except for large animal items carried in bill tip; female emerges from nest c. 4 weeks before chicks fledge; fledging period undocumented, probably c. 55 days.

**Movements.** Seasonal post-breeding movement in Sept-Oct, from lowland forest into hills for non-breeding season.

**Status and Conservation.** Not globally threatened. Restricted-range species: present in Sri Lanka EBA. Common resident in moister lowland forest, more local elsewhere. Occurs in several small reserves, and also extends into gardens and plantations.

**Bibliography.** Ali (1935-1937), Ali & Ripley (1983), Ginige (1998), Grimmer *et al.* (1998), Harrison (1999), Henry (1998), Hoffmann (1998), Hoffmann *et al.* (1995), Inskipp *et al.* (1996), Jones *et al.* (1998), Kazmierczak (2000), Kemp (1976a, 1988), Lamsfuss (1998), Legge (1983), Phillips (1978, 1979), Poonswad (1993b), Punchihewa (1968), Ripley (1982), Samaraweera (1987), Stattersfield *et al.* (1998), de Zylva (1984).

### 22. Indian Grey Hornbill

*Ocyrceros birostris*

**French:** Calao de Gingi

**German:** Keilschwanztoko

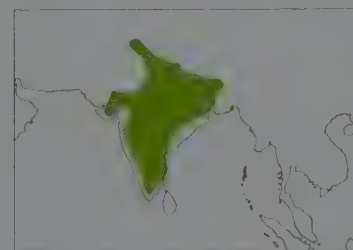
**Spanish:** Cálao Gris Indio

**Other common names:** Grey(!)/Common Grey Hornbill

**Taxonomy.** *Buceros birostris* Scopoli, 1786, Pondicherry, India.

Genus sometimes combined with African *Tockus*, but differs in feeding behaviour at nest. Monotypic.

**Distribution.** NE Pakistan, S Nepal and NW Bangladesh S through most of India (except SW and E coasts).



**Descriptive notes.** 50 cm; male 375 g. Small, silvery-grey and white hornbill, tail long and graduated with dark and light tip. Male has blackish bill and narrow casque, latter with protruding front edge, bill tip and much of lower mandible pale yellow; bare skin around eyes grey, eyes red-brown. Female smaller, casque and anterior protrusion both less prominent; lacks white tips to primaries; iris browner. Juvenile with small, pale yellow, casqueless bill.

**Habitat.** Deciduous woodland, parkland and open thorn-forest, especially among scattered fig trees and in areas of rural cultivation or gardens.

**Food and Feeding.** Mainly small fruits, especially figs; also takes various insects, lizards, mice and nestlings; rarely, flower petals. Flies from tree to tree in search of food; sometimes descends to hop about on ground, or flies up to hawk insects.

**Breeding.** Little known. Lays mainly in Feb or May-Jun, at end of dry season. Possibly co-operative at times, with additional male helpers. Nest in natural cavity 3-13 m up in indigenous or exotic tree, lined with bark flakes; female seals nest entrance with own droppings and food, but male also delivers some mud. Clutch 2-5 eggs, following pre-laying period 7-10 days; incubation at least 21 days; female moults remiges and rectrices together while breeding, but emerges from nest c. 1 week before chicks fledge; fledging at least 45 days.

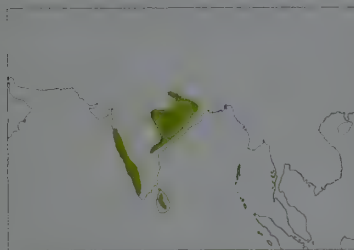
**Movements.** Generally resident, except for some local movements to keep track of fruiting trees; at such times, occasionally reported in small flocks of up to 30.

**Status and Conservation.** Not globally threatened. Widespread, and often common in wide range of habitats. Extensive range includes several reserve areas. Also co-exists well with human rural development, and appears reasonably adaptable. Frequent competition for nest-holes with Rose-ringed Parakeets (*Psittacula krameri*), when generally dominant, and even eats that species' chicks and throws out nest lining.

**Bibliography.** Abdulali (1974a), Ali (1996), Ali & Ripley (1983), Amladi & Daniel (1973), Baker (1934a), Daniels (1997), Finlay (1928), Grewal (1995), Grimmer *et al.* (1998), Hall (1918), Harvey (1990), Hutchinson (1943), Inskipp, C. (1989), Inskipp, C. & Inskipp (1991), Inskipp, T. *et al.* (1996), Kemp (1976a, 1988), Lowther (1942), MacDonald (1960), Mahabal & Lamba (1987), Majumdar *et al.* (1992), Neelakantan (1953), Newham (1911), Osborn (1904), Patil *et al.* (1997), Poonswad (1993b), Ripley (1982), Roberts (1991, 1996), Sant (1996), Santharam (1990), Sultana & Khan (2000).







after fallen fruit, or to chase insects. Usually forages in small flocks, but often many (up to 58 recorded) gather at localized food sources and roost communally.

**Breeding.** Lays in Mar-Sept, mainly during rainy season. Nest in natural cavity 3.5-15 m up in tree, sealed by female with little help from male. Clutch 2-4 eggs; incubation 29-30 days; female moults remiges and rectrices once enclosed, may emerge from nest when oldest chicks anything from 10 days to 35 days old; fledging 49 days.

**Movements.** Generally considered sedentary in India, with only local movements in search of food; reported to move from lowlands into hills in Sri Lanka.

**Status and Conservation.** Not globally threatened. CITES II. Currently considered Near-threatened. General decline in numbers throughout range, especially in W India and Sri Lanka; now rare in Kerala. Habitat destruction is main threat, so species common only in areas of low human population density, including a few reserves; these include Rajiv Gandhi National Park (Nagarhole), in India, and Uda Walawe National Park and Yala National Park, in Sri Lanka. Reportedly collected for medicinal purposes in Orissa, in E India. Captive-breeding programme has been initiated.

**Bibliography.** Alday (1997), Ali (1996), Ali & Ripley (1983), Daniels (1997), Dev (1992-1993), Frith & Frith (1983a), Gaston & Zacharias (1996), Ginige (1998), Gokula & Vijayan (1997), Grimmer et al. (1998), Harrison (1999), Henry (1998), Inskipp et al. (1996), Kazmierczak (2000), Kemp (1976a, 1988), Lamsfuss (1998), Legge (1983), Modse (1988), Osmaston (1913), Phillips (1978, 1979), Pitman (1913), Poonswad (1993b), Reddy & Basalingappa (1995), Reddy et al. (1990), Ripley (1982), Sanjeevareddy (1988), Stattersfield & Capper (2000), Wright (1992), Zacharias & Gaston (1999).

## 24. Oriental Pied Hornbill

### *Anthracoceros albirostris*

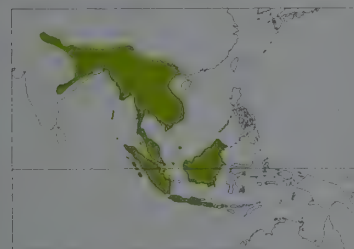
**French:** Calao pie **German:** Orienthornvogel **Spanish:** Calao Cariblanco  
**Other common names:** Pied(!)/Asian Pied/Northern Pied Hornbill; Malaysian Pied/Sunda Pied Hornbill (*convexus*)

**Taxonomy.** *Buceros albirostris* Shaw and Nodder, 1790, Chandernagore, India. Forms a superspecies with *A. coronatus* and *A. marchei*. Was long confused with *A. coronatus*, with complex synonymy of both scientific and vernacular names; the two were considered conspecific, but now recognized as two distinct species that differ in size and in several aspects of morphology (including colour of bare throat skin) and behaviour, and which overlap in range without interbreeding. During period of confusion, present species was commonly referred to as *A. malabaricus*, but, although two years senior to *albirostris*, this name appears to be unidentifiable; within "*A. malabaricus*", E birds were sometimes separated as race *leucogaster*, but this name now considered a junior synonym of *albirostris*. Race *convexus* sometimes considered a separate species, but alleged sympatry without hybridization is apparently not proven, and supposed difference in tail pattern not constant. Two subspecies recognized.

#### Subspecies and Distribution.

*A. a. albirostris* (Shaw & Nodder, 1790) - N India and S Nepal E to S China (Yunnan, SW Guangxi), and S to N Peninsular Malaysia, SW Cambodia and S Vietnam.

*A. a. convexus* (Temminck, 1831) - Peninsular Malaysia, Sumatra, Borneo, Java and Bali, including numerous smaller islands.



**Descriptive notes.** 55-60 cm; male 680-907 g, female 567-879 g. Medium-sized, pied hornbill with white belly and trailing edge to wings. Male nominate race with white tips to outer tail feathers, central pair rarely with narrow white tips; bill pale yellow with black base of lower mandible; large casque tapering to projecting anterior blade, pale yellow with black base, black patch at front extending variably on to culmen; bare circumorbital skin and bare throat patch bluish-white; eyes dark red. Distinguished from *A. coronatus* by smaller size, less black on casque, pale blue (not pink-tipped) throat skin. Female smaller, casque

without anterior projection, more black on smaller bill, eyes browner. Juvenile less glossy black, casque undeveloped, bill small and all pale yellow. Race *convexus* slightly larger, usually less black on bill (variable), typically shows tail pattern of *A. albirostris*, but this feature is somewhat variable.

**Habitat.** Edges of evergreen forest, and various types of open deciduous forest, woodland and plantations, at up to 700 m. Forages into surrounding areas of open secondary forest and cultivation.

**Food and Feeding.** Mainly fruit, also small animals. Fruits from at least 35 species recorded eaten in Thailand, with more non-fig than fig species. Animals include various insects, centipedes, millipedes, scorpions, spiders, snails, earthworms, lizards, small birds and rats; occasionally, even takes fish and crabs from water. Forages mainly among foliage, although often descends to ground. Picks off any small animals, or catches them in flight. Feeds as territorial families, or gathers in flocks of up to 50 in non-breeding season.

**Breeding.** Lays in Feb-Apr on Asian mainland, and in Sept-Mar, even May, on Malaysian and Indonesian islands. Territorial in pairs. Nest in natural cavity 2-30 m up in tree, often *Dipterocarpus* or *Syzgyium* species, or rarely in limestone cliff; female does most of nest preparation and sealing. Clutch 1-3 eggs; incubation 25-27 days; female moults remiges and rectrices after enclosure, emergence varies from point at which chicks fledge to 20 days before; fledging 49-55 days.

**Movements.** Sedentary in most areas; some flock formation and local movements during non-breeding season, and to track fruiting trees in some marginal areas.

**Status and Conservation.** Not globally threatened. CITES II. The commonest Asian hornbill in most areas across its wide range. Home range in Thailand only c. 15 km<sup>2</sup>. Adaptable, utilizes wide range of forest and modified habitats, including in several extensive protected areas, e.g. Khao Yai

National Park (Thailand); able to co-exist with various forms of land use, provided at least some forest remains, and nests in relatively small trees when necessary. Kept as pet or hunted for food in many areas, but still generally common.

**Bibliography.** Ali (1996), Ali & Ripley (1983), Ali et al. (1996), Allen (1919), Bangs & Van Tyne (1931), Bartels & Bartels (1937), Chak Sokhaviheaboth (1998), Chaudhary (1998), Chaulia et al. (1998), Cheng Tsohsin (1973), Datta (1998), Deignan (1945), Duckworth (1996), Duckworth et al. (1999), Eames & Robson (1992), Ellis (1998), Étchécopar & Hùe (1978), Frith & Douglas (1978), Frith & Frith (1978, 1983a), Gee (1933a, 1933b), Ghosh (1994), Grimmer et al. (1998), Holmes et al. (1993), Hutchins (1976), Inskipp, C. & Inskipp (1991), Inskipp, C., Inskipp & Grimmer (1999), Inskipp, T., Lindsey & Duckworth (1996), Jeyarajasingam & Pearson (1999), Kaprielian et al. (1996), Kemp (1976a, 1988), Lan Yang & Xianji Wen (1993), Lekagul & Round (1991), Li Hanhua (1983), Li Hanhua & Shen Lantian (1983), MacKinnon & Philipps (1993, 2000), Madoc (1976), van Marle & Voous (1988), Medway & Wells (1976), Nazimuddeen (1994), Ng Soonchye et al. (1998), Pan Khangaun (1987b), Poonswad (1993b, 1995), Poonswad, Chimchome et al. (1998), Poonswad, Tsuji, Jirawatkavi & Chimchome (1998), Poonswad, Tsuji & Ngarmpongsoi (1983, 1986, 1987), Primrose (1921), Reinhard & Strehlow (1998), Riley (1938), Ripley (1982), Robson (2000a), Round (1985, 1988), Seibels (1989), Shen Lantian & Li Hanhua (1981), Singh (2000), Smythies (1986, 1999), Stepanyan (1995), Tikader (1983), Tonge (1996), Tsuji et al. (1987), Wang Sung (1998), Wells (1999), Wells & Medway (1976), Wong Hongmun & Khin Maynyunt (1998), Zhao Zhengjie (1995).

## 25. Palawan Hornbill

### *Anthracoceros marchei*

**French:** Calao de Palawan **German:** Palawanhornvogel **Spanish:** Calao de Palawan

**Taxonomy.** *Anthracoceros marchei* Oustalet, 1885, Palawan, Philippines.

Forms a superspecies with *A. coronatus* and *A. albirostris*. Monotypic.

**Distribution.** Calamian Is (Busuanga, Calawit and Culion), Palawan and Balabac I.



**Descriptive notes.** 55 cm; male 580-920 g. Medium-sized hornbill with all-black plumage, apart from white tail. Male has pale ivory-yellow casque and bill, with black base to lower mandible; bare skin around eye and on throat white, tinged blue; eyes reddish-brown, black orbital ring. Female smaller; has smaller bill and casque with greyish wash; dark grey-brown eyes. Juvenile with even smaller, paler bill with grey base, no black ring around dark grey eye.

**Habitat.** Inhabits primary and secondary evergreen forest; also enters mangrove swamps and sometimes observed in areas of subsistence

farming; occurs up to 900 m.

**Food and Feeding.** Mainly fruit, but insects and lizards also recorded in diet. Forages at any level, from canopy to ground, usually in small groups; groups detected by flapping noises or shrill, raucous calls.

**Breeding.** Virtually nothing known. Male in breeding condition in Apr; one nest was photographed c. 20 m up in large tree, the entrance sealed and female inside with chicks, but no date or location recorded.

**Movements.** Probably sedentary in restricted island habitats.

**Status and Conservation.** VULNERABLE. CITES II. Restricted-range species: present in Palawan EBA. Fragmented range, on no more than five islands, the three smallest of which are now largely cleared of forest. Currently reported as relatively common only at St Paul's Subterranean River National Park, on Palawan. Whole island of Palawan is a Biosphere Reserve, with hunting prohibited, but enforcement of protective laws is difficult. Species known still to be collected from nest for food and for pet trade, and much of remaining forest still seriously threatened by logging and mining activities. Urgent need for further survey, study of life history and biology, and studies of captive individuals. The only hornbill species in the Palawan group.

**Bibliography.** Collar et al. (1999), Dickinson et al. (1991), Forshaw & Cooper (1994), Frith & Douglas (1978), Frith & Frith (1983a), Gonzales & Rees (1988), Hiddinga (1996b), Inskipp et al. (1996), Kemp (1976a, 1988, 1995a), Kennedy et al. (2000), duPont (1971), Sanft (1960), Stattersfield & Capper (2000), Stattersfield et al. (1998), Worth et al. (1994).

## 26. Black Hornbill

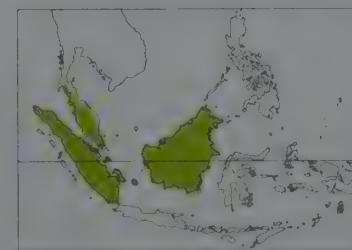
### *Anthracoceros malayanus*

**French:** Calao charbonnier **German:** Malaiehornvogel **Spanish:** Calao Malayo  
**Other common names:** Asian/Malay Black Hornbill

**Taxonomy.** *Buceros malayanus* Rafines, 1822, Malacca.

Monotypic.

**Distribution.** S Thailand (S from Trang), Peninsular Malaysia, Lingga Archipelago (Singkep), Sumatra, including Bangka I and Belitung I, and Borneo.



**Descriptive notes.** 60-65 cm; male 1050 g. Medium-sized to largish mostly black hornbill with elongated central tail feathers, which are sometimes tipped white, outer tail with broad white tips; white or pale grey supercilary stripe in 85% of individuals, dark grey or absent in 15%. Male with pale yellow bill and casque, latter projecting in thin blade; bare skin around eye and small bare throat patches blue-black; eyes dark red. Female smaller, bill and small casque black, circumorbital skin yellowish-flesh to pinkish, throat patches yellow-buff, eyes paler. Juvenile with relatively small, pale green bill.

**Habitat.** Inhabits lowland primary evergreen forest, usually below 200 m; also found in adjacent gallery forest, tidal swamp-forest and tall secondary forest.

**Food and Feeding.** Mainly larger lipid-rich fruits; fewer figs, but of at least 17 species; also some small animals, including insects, occasionally bats, and bird eggs. Feeds mainly in middle and lower strata of forest, and often forages also among dense tangles; early-morning visitor to fruiting trees. Uses bill to split husks and to prise off bark. Catches bats emerging from caves at dusk, and feeds these to juveniles.

**Breeding.** Little known. Laying aseasonal, recorded in Jan-Feb, Apr, Aug and Nov-Dec; does not always breed annually. Nest in natural cavity, or, possibly, in woodpecker hole, in tree. In captivity, 2-3 eggs; incubation c. 30 days; chick retains pinkish-yellow skin throughout nestling period; male feeds female and chicks throughout cycle, resuming regular harsh calling only after breeding; fledging c. 50 days; each adult attends separate chick after fledging.

**Movements.** Apparently sedentary and territorial; only rarely forms flocks, of up to 33 birds, often mainly immatures.

**Status and Conservation.** Not globally threatened. CITES II. Currently considered Near-threatened. Widespread, but only locally common, and somewhat restricted by specific habitat requirements. Occurs at densities of 1 pair/0.6-5 km<sup>2</sup>. Present in Way Kambas National Park, in Sumatra. Predominance in flat lowlands makes species vulnerable to habitat destruction, especially in Sumatra and Malay Peninsula.

**Bibliography.** Andrew (1992), Bartels & Bartels (1937), Becker & Wong (1985), Danielsen & Heegaard (1995), Frith & Douglas (1978), Frith & Frith (1983a), Galetti & McConkey (1998), Hall (1996b), Holmes *et al.* (1993), Inskipp *et al.* (1996), Jeyarajasingam & Pearson (1999), Johns (1987, 1988), Kemp (1976a, 1988), Lambert (1989), Leighton (1982, 1986), Leighton & Leighton (1983), Lekagul & Round (1991), MacKinnon & Philipps (1993), Madoe (1976), van Marle & Voous (1988), Medway & Wells (1976), Miller (1998), Poonswad (1993b), Riley (1938), Robson (2000a), Round (1985, 1988), Scheres & Alba (1997), Smythies (1999), Stattersfield & Capper (2000), Vowles & Vowles (1984), Wells (1999), Wilkinson, Dutton & Sheldon (1991), Wong Hongmun & Khin Maynyunt (1998), Worth *et al.* (1994), van Zyl & Kemp (1998).

## 27. Sulu Hornbill

### *Anthracoceros montani*

**French:** Calao des Sulu

**German:** Suluhornvogel

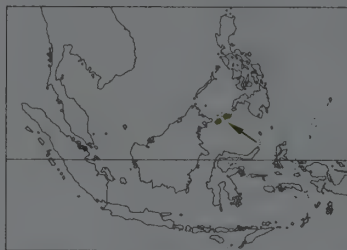
**Spanish:** Cálao de las Sulu

**Other common names:** Montano's Hornbill

**Taxonomy.** *Buceros Montani* Oustalet, 1880, Sulu Archipelago.

Relationships with congeners uncertain. Monotypic.

**Distribution.** Islands of Jolo (probably extinct) and Tawitawi, in Sulu Archipelago; recently recorded also on Tandubatu, Dundangan and Baliungan.



**Descriptive notes.** 50 cm. Medium-sized hornbill, all black but for white tail. Male with bill and blade-like casque black; bare skin around eye and bare throat skin black; eyes creamy. Female smaller, bill and casque smaller, eyes dark brown. Juvenile with smaller bill plain greenish-yellow, no casque, grey circumorbital skin.

**Habitat.** Evergreen dipterocarp forest, in lowland and highlands.

**Food and Feeding.** Reported to eat fruit, small lizards and some insects, but few details. Recorded in pairs at fruiting trees in forest, or visiting isolated trees among cultivation.

**Breeding.** No documented information. On Tawitawi, pair with immature seen in Sept; nest in tall, large-diameter tree; reported clutch size 2, with fledging reported in May-Jun.

**Movements.** Probably sedentary.

**Status and Conservation.** CRITICAL. CITES II. Restricted-range species: present in Sulu Archipelago EBA. Probably the world's most threatened hornbill species. Population currently estimated at fewer than 20 pairs in main mountain range on Tawitawi; no records from Jolo since 1883, and probably extinct here; formerly rare on Sanga Sanga I, now almost certainly extinct. Islands of Sulu Archipelago, where this is the only hornbill present, were relatively little logged until recently, and species was considered common to abundant; by 1994, however, Jolo had been logged, resulting probably in disappearance of the last hornbills here, and remaining forest on main island of Tawitawi was being rapidly logged and species was rare and local, with last degraded patches of lowland forest planned for conversion to oil-palm plantations; in 1995, reported from small islands of Tandubatu, Dundangan and Baliungan, in Tawitawi group, but in very low numbers. Is still hunted for food, cagebird trade and exhibition, especially on Tawitawi. Suspected to have been widely shot during human armed conflict in early 1970's, both for food and merely for target practice; continuing political unrest poses serious obstacles to any conservation work. Surveys, and studies of species' life history and biology, including captive studies, urgently needed to prevent its imminent extinction.

**Bibliography.** Anon. (1997a), Collar & Andrew (1988), Collar, Crosby & Stattersfield (1994), Collar, Mallari & Tabaranza (1999), Delacour & Mayr (1946), Dickinson *et al.* (1991), Diesmos & Pedragosa (1995), Dutton *et al.* (1996), Frith & Frith (1983a), Inskipp *et al.* (1996), Kemp (1976a, 1988), Kennedy *et al.* (2000), Lambert (1993), McGregor (1909-1910), duPont (1971), du Pont & Rabor (1973a), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Worth *et al.* (1994).





28



*ssp rhinoceros*

29

*ssp silvestris*



*ssp borneoensis*

31



*ssp hydrocorax*

*ssp semigaleatus*

30

*ssp mindanensis*

PLATE 39

inches 8  
cm 20



# Genus *BUCEROS* Linnaeus, 1758

## 28. Great Hornbill

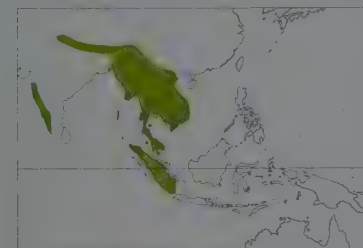
### *Buceros bicornis*

**French:** Calao bicorne **German:** Doppelhornvogel **Spanish:** Cálao Bicorné  
**Other common names:** Great Indian/Great Pied/Giant Hornbill, Concave-casqued Hornbill

**Taxonomy.** *Buceros bicornis* Linnaeus, 1758, Bengkulu, Sumatra.

Forms a superspecies with *B. rhinoceros*. Hybridization with latter reported both in wild and in captivity. Birds from Asian mainland have been separated as race *homrai* on basis of larger size, but variation seems to be clinal; SW Indian population described as race *cavatus*, but apparently inseparable from those in N of Subcontinent. Monotypic.

**Distribution.** Western Ghats (SW India); S Himalayas (Garhwal and Kumaon) E to NC Myanmar, S China (W Yunnan) and Vietnam, and S to Malay Peninsula and Sumatra.



**Descriptive notes.** 95-105 cm; male 2600-3400 g, female 2155-3350 g. Very large, pied hornbill with black band across white tail; long, deep bill, and white plumage areas of head, neck and wing-coverts, usually cosmetically coloured yellow with green oil. Male has flat casque double-pointed at front, with black rim; black-rimmed red eyes. Female smaller, casque smaller and without black; eyes white, with red rim that flushes brighter when breeding. Juvenile with blue-grey eyes, and small casqueless bill which grows to maturity over 5 years.

**Habitat.** Large tracts of primary evergreen forest, but will cross open areas between forest patches; occurs at up to 2000 m.

**Food and Feeding.** Mainly fruit, rarely flowers and buds; also many large insects and other arthropods, besides various small reptiles, birds and mammals. Eats many species of fig, which comprised 73% of food delivered to nests in India; also drupes of *Vitex*, and various other lipid-rich fruits from at least 18 genera. Feeds mainly in canopy, but will descend to ground for fallen fruit. Usually feeds in pairs or family groups, but sometimes gathers in numbers at fruiting trees and roosts in flocks of up to 200 in non-breeding season.

**Breeding.** Lays in Jan-Apr across whole range. Monogamous and territorial, sometimes engaging in aerial casque-butting. Nest in natural hole 8-35 m up in larger forest tree, often *Dipterocarpus* or *Swyngium* species, rarely in hole in limestone cliff; entrance often elongate, sealed by both sexes. Usually 2 eggs (1-4), laid at intervals of 4-5 days, after pre-laying period 1-4 days; incubation 38-40 days, in captivity 35-37 days recorded; chick 45-50 g at hatching; female and chicks fed in nest by male, with up to 185 items daily, or 43 g per hour, regurgitated from gullet; female moults remiges and rectrices once enclosed, usually emerges when oldest chick 14-59 days old, well before it fledges; fledging 72-96 days; total nesting cycle 102-140 days; in captivity, however, recorded nestling period 70-74 days, female emerging few days before chick and after 4 months of enclosure, having undergone successional and incomplete moult of main wing and tail feathers. Recorded longevity in captivity over 41 years.

**Movements.** Largely sedentary; ranges more widely for food in non-breeding season, but without any regular pattern.

**Status and Conservation.** Not globally threatened. CITES I. Currently considered Near-threatened. Spread over wide range, but declining in many areas, especially in W India (estimated 3500 birds in 100 forest patches) and Sumatra. Family home range may extend over more than 600 km<sup>2</sup>, in which case species never really abundant locally; in Thailand, however, breeding home range only 3-7 km<sup>2</sup> and non-breeding 14-7 km<sup>2</sup>. Occurs in several protected areas throughout range, e.g. Indira Gandhi (Top Slip) and Periyar National Parks (India), Khao Yai National Park (Thailand) and Way Kambas National Park (Sumatra). Habitat degradation is main cause of decline, in addition to population fragmentation and widespread loss of large nest trees; also subject to hunting and trapping in most areas, for food, tribal medicinal use and trade. Has been bred several times in captivity.

**Bibliography.** Ali (1996), Ali & Ripley (1983), Ali *et al.* (1996), Bangs & Van Tyne (1931), Bingham (1897), Bohmke (1987), Brouwer (1990), Buri (1996), Chak Sokhaviheebath (1998), Chaudhary (1998), Chaulua *et al.* (1998), Cheng Tsohsin (1973), Choy (1978, 1980), Datta (1998), Davidson (1988), Deignan (1945), Derks (2000), Duckworth *et al.* (1999), Eames & Robson (1992), Ellison (1923), Fleming (1968), Frith & Douglas (1978), Galana (1997), Ghosh (1994), Golding & Williams (1986), Grimmett *et al.* (1998), Holmes *et al.* (1993), Horne (1869), Hutton (1986), Inskipp & Inskipp (1991), Inskipp *et al.* (1999), James & Kannan (1996), Jeyarajasingam & Pearson (1999), Kannan (1994a, 1994b, 1994c), Kannan & James (1997, 1998, 1999), Kemp (1976a, 1988), Kinloch (1923), Lan Yang & Xianji Wen (1993), Law (1928), Lekagul & Round (1991), MacKinnon & Phillips (1993, 2000), Madoc (1976), van Marle & Voous (1988), McClure (1970), Medway & Wells (1976), Nehls (2000), Phipson (1989), Poonswad (1993b, 1995), Poonswad & Tsuji (1994), Poonswad, Chimchome *et al.* (1998), Poonswad, Tsuji, Jirawatkavi & Chimchome (1998), Poonswad, Tsuji & Ngampongso (1983, 1986, 1987), Poulsen (1970), Prater (1921), Preuss & Preuss (1973), Riley (1938), Ripley (1982), Robiller & Trogisch (1985), Robson (2000a), Round (1985, 1988), de Ruiter (1998a), Scheres & Alba (1997), Shankar Raman (1998), Singh (2000), Smythies (1986), Spence (1920), Stattersfield & Capper (2000), Stepanyan (1995), Stott (1951), Thewlis *et al.* (1998), Thormahlen & Healy (1990), Tickell (1864), Tikader (1983), Tsuji *et al.* (1987), Uehara (1990), Wells (1999), Wong Hongmun & Khin Maynyunt (1998), Wood (1927), Yeung (1997), Youth (1995), Zacharias & Gaston (1999), Zhao Zhengjie (1995).

## 29. Rhinoceros Hornbill

### *Buceros rhinoceros*

**French:** Calao rhinocéros **German:** Rhinozeroshornvogel **Spanish:** Cálao Rinoceronte  
**Other common names:** Great Rhinoceros Hornbill

**Taxonomy.** *Buceros Rhinoceros* Linnaeus, 1758, India; error = Malacca.

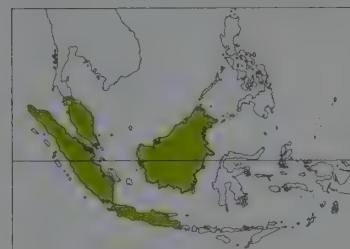
Forms a superspecies with *B. bicornis*. The two are reported to have hybridized both in wild and in captivity. Birds from Sumatra described as race *sumatranus*, on grounds of larger size, but appear inseparable from nominate. Three subspecies currently recognized.

**Subspecies and Distribution.**

*B. r. rhinoceros* Linnaeus, 1758 - S Thailand, Peninsular Malaysia and Sumatra.

*B. r. borneensis* Schlegel & S. Müller, 1840 - Borneo.

*B. r. silvestris* Vieillot, 1816 - Java.



**Descriptive notes.** 80-90 cm; male 2465-2960 g, female 2040-2330 g. Large mainly black hornbill with white thighs and vent, black band across white tail; bill and casque cosmetically coloured orange and red with green oil. Male nominate race with large casque black at base, more or less recurved at tip; black-rimmed red eyes. Female smaller, casque smaller and without black, red-rimmed white eyes. Juvenile with small, casqueless bill, blue-grey eyes. Race *borneensis* smaller, with shorter and broader casque more sharply recurved at tip; *silvestris* with broader black tailband, anterior casque normally not rolled back.

**Habitat.** Extensive areas of primary evergreen forest, extending into tall secondary forest; often crosses more open habitats; occurs at up to 1400 m.

**Food and Feeding.** Mainly fruits, especially figs, but also various lipid-rich capsules and drupes; in addition, eats any small animals it can capture, mostly arthropods, but also lizards, tree-frogs and bird eggs. Usually forages in pairs; sometimes in small flocks when not breeding.

**Breeding.** Lays aseasonally, in Jan, Mar-Jun, Sept and Nov. Indication that sometimes breeds co-operatively, both in wild and in captivity. Nest in natural cavity 9-15 m up in tall forest tree, probably rarely in limestone cliff; entrance hole often an elongated slit. Clutch 1-2 eggs; incubation 37-46 days; male feeds nest occupants by regurgitating multiple food items from gullet; female moults remiges and rectrices after enclosure, emerges 39-51 days after chicks hatch; fledging 78-80 days.

**Movements.** Breeding pairs sedentary in many areas; in non-breeding period, may make long movements in search of fruiting trees, especially immature birds in flocks of up to 25.

**Status and Conservation.** Not globally threatened. CITES II. Currently considered Near-threatened. Occurs in several large mainly lowland reserves, including Taman Negara National Park (Malaysia), Gunung Leuser and Way Kambas National Parks and Berbak Game Reserve (Sumatra) and Danum Valley Conservation Area (Borneo), but always at low densities. Distribution and numbers reduced in many areas over wide range, mainly through cutting of forest for timber and agriculture. Hunted in many areas for the bill and tail feathers, which are used in ceremonial dress; also captured for trade and for food.

**Bibliography.** Andrew (1985, 1992), Anggraini *et al.* (2000), Anon. (1990), Bartels & Bartels (1937), Bennett *et al.* (1997), Cranbrook & Kemp (1995), Frith & Douglas (1978), Frith & Frith (1983b), Harrison (1951), Hetharia (1941), Holmes *et al.* (1993), Jeyarajasingam & Pearson (1999), Johns (1982, 1987, 1988), Kemp (1976a, 1988), Leighton (1982, 1986), Leighton & Leighton (1983), Lekagul & Round (1991), MacKinnon & Phillips (1993), Madoc (1976), van Marle & Voous (1988), McClure (1966), Medway & Wells (1976), Meyer de Schauensee & Ripley (1940), Poonswad (1993b), Primm (1996), Reilly (1988a, 1988b), Riley (1938), Robson (2000a), Round (1985, 1988), Scheres & Alba (1997), Schutz & Urban (1997), Shelford (1899), Smythies (1999), Stattersfield & Capper (2000), Uehara (1990), Vowles & Vowles (1984), Wells (1999), Wilkinson, Dutson & Sheldon (1991).

## 30. Rufous Hornbill

### *Buceros hydrocorax*

**French:** Calao à casque plat **German:** Feuerhornvogel **Spanish:** Cálao Filipino Grande  
**Other common names:** Great Philippine Hornbill, Philippine Brown Hornbill

**Taxonomy.** *Buceros Hydrocorax* Linnaeus, 1766, Moluccas; error = Manila, Philippines.

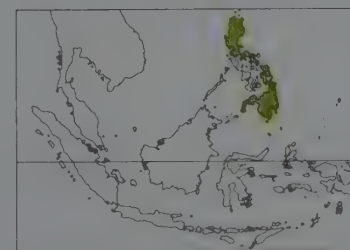
Races *mindanensis* and *semigaleatus* rather distinct from nominate, and together may represent a separate species. Basilan birds described as race *basilanicus*, but appear inseparable from *mindanensis*. Three subspecies currently recognized.

**Subspecies and Distribution.**

*B. h. hydrocorax* Linnaeus, 1766 - N Philippines, on Luzon and Marinduque.

*B. h. semigaleatus* Tweeddale, 1878 - C Philippines, on Samar, Leyte, Bohol, Panaon, Buad, Calicoan and Biliran.

*B. h. mindanensis* Tweeddale, 1877 - S Philippines, on Dinagat, Siargao, Balut, Bucas, Talicud, Mindanao and Basilan.



**Descriptive notes.** 60-65 cm; male 1345-1824 g, female 1171-1662 g. Large hornbill, rufous, brown and black, with all-white tail which is often stained pale tan; bill and casque coloured cosmetically with red green oil. Male nominate race with black-based red bill, large red casque with distal projection; bare skin around eye yellow; eyes red, sometimes pale bluish; feet reddish-brown. Female smaller, casque smaller, no black on bill base, circumorbital skin black, eyes whitish. Juvenile very different, mainly off-white with grey-brown wings and tail base, black band across central tail, small casqueless bill black, eyes brown. Other

races smaller than nominate, with small patch of bare throat skin: *mindanensis* with outer half of bill pale yellow, circumorbital skin black with only lower part yellow, yellow throat skin, eyes pale bluish in both sexes, legs redder, juvenile tail with black base and no clear central band; *semigaleatus* similar, but casque much smaller, female has circumorbital and throat skin greenish-yellow, juvenile as previous.

**Habitat.** Primary evergreen forest, locally also tall secondary forest; occurs at up to 2100 m.

**Food and Feeding.** Mainly fruits and seeds, including figs and feral guava; also insects and centipedes. Forages in canopy, but sometimes comes down to low bushes or even the ground; insects also pursued in flight.

**Breeding.** Little known. Lays Jan-May. Co-operative, in groups of 3-7 birds; all chase off conspecifics and other hornbills from nest area. Nest in natural hole 14-30 m up in trunk of large tree. Clutch 2-4 eggs; all group-members feed female and chicks in nest; no information on incubation and fledging periods.

**Movements.** Apparently chiefly sedentary, as suggested by shorter, narrower wings than other *Buceros*; at times gathers, moves and roosts in small communal flocks with *Aceros leucocephalus*.

**Status and Conservation.** Not globally threatened. CITES II. Currently considered Near-threatened. Occurs on a number of islands in Philippines, on all of which forest habitat has been lost, reduction in forest cover ranging from 70% on Luzon and Mindanao to even more on other islands, especially smaller ones; still locally common, e.g. in Sierra Madre Mts of E Luzon. Occurs in Quezon National Park, on Luzon. Recently reported to have declined drastically on Luzon, which has the most extensive remaining forest. Especially vulnerable because of large size and naturally low densities. Still hunted for food, trade, and to make traditional head-dresses. Conservation status may require reassessment. If actually two separate species, each with a much smaller effective population, then both could be considered potentially threatened.

**Bibliography.** Curl (1911), Danielsen *et al.* (1994), Delacour & Mayr (1946), Dickinson *et al.* (1991), Gilliard (1950a), Gonzales & Rees (1988), Goodman & Gonzales (1990), Inskipp *et al.* (1996), Kemp (1976a, 1988), Kennedy *et al.* (2000), Lint & Stott (1948), Manuel (1969), McGregor (1909-1910), duPont (1971), duPont & Rabor (1973b), Poonswad (1993b), Potter (1953), Poulsen (1995), Rand & Rabor (1960), Stattersfield & Capper (2000), Stott (1947), Witmer (1988a, 1988b, 1993), Worth *et al.* (1994).

## Genus *RHINOPLAX* Gloger, 1841

### 31. Helmeted Hornbill

#### *Rhinoplax vigil*

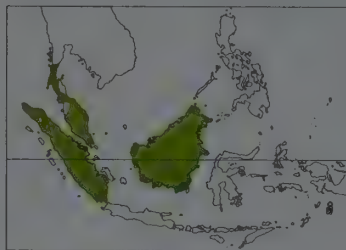
French: Calao à casque rond      German: Schildschnabel      Spanish: Cálao de Yelmo  
Other common names: Great Helmeted Hornbill, Solid-billed Hornbill

**Taxonomy.** *Buceros vigil* J. R. Forster, 1781, Sumatra.

Often placed in genus *Buceros*, but differs clearly in morphology, and in unique hooting call ending in loud cackle. Monotypic.

**Distribution.** S Myanmar and S Thailand through Malay Peninsula to Sumatra and Borneo.

**Descriptive notes.** 110-120 cm; male 3060 g, female 2610-2840 g. Distinctive, very large hornbill, mostly dark brown and white with long central tail feathers, relatively short bill cosmetically col-



oured red with green oil. Male with bare red areas on neck; bill, and high casque with heavy anterior buttress of "ivory", yellow at front; eyes dark red. Female smaller, with pale turquoise skin on head and neck. Juvenile with shorter central rectrices, small yellow bill, low casque, bare head and neck light greenish-blue.

**Habitat.** Inhabits primary evergreen forest, especially in foothills, but able to use some selectively logged forest; typically occurs at up to 1100 m, occasionally 1500 m.

**Food and Feeding.** Mainly fruit, especially figs, but about half of each day spent hunting small animals, including squirrels, snakes,

birds, even smaller hornbill species. Forages mainly in canopy of tall trees; suspected to dig under bark and into soft wood and crevices, sometimes hanging almost upside-down. Pair-members hunt separately within home range.

**Breeding.** Little known. Lays aseasonally, in Jan-Mar, May and Nov. Territorial in pairs, with aerial casque-butting in aggression. Nest in natural hole in tall tree; entrance sealed with mud and food remains, and floor lined with wood chips. Clutch 1-2 eggs, but only 1 fledgling recorded with adults; female fed in nest by male, with food carried in gullet and regurgitated, except for some larger animals carried in bill tip; incubation and fledging periods not documented.

**Movements.** Apparently largely sedentary and territorial; small groups of up to 14 non-breeding and immature birds wander locally in search of food.

**Status and Conservation.** Not globally threatened. CITES I. Currently considered Near-threatened. Range has contracted in many areas through forest removal, though species still locally not uncommon in unlogged forest; extinct in Singapore by 1950. Favours rugged terrain, and occurs in several large reserves. Present in Gunung Mulu National Park (Peninsular Malaysia), in Gunung Leuser, Kerinci-Seblat and Way Kambas National Parks (Sumatra), and in Danum Valley Conservation Area (Borneo). Very shy and wary, having been commonly hunted for centuries; casque and tail feathers still widely collected for sale and decoration. Difficult to maintain in captivity.

**Bibliography.** Andrew (1992), Anggraini *et al.* (2000), Banks (1935), Bartels & Bartels (1937), Bennett *et al.* (1997), Camman (1951), Collar & Andrew (1988), Cranbrook & Kemp (1995), Danielsen & Heegaard (1995), Davison (1995), Haimoff (1987), Harrison (1951), Hetharia (1941), Holmes *et al.* (1993), Jeyarajasingam & Pearson (1999), Johns (1988), Kemp (1976a, 1988), King (1978/79), Leighton (1982, 1986), Leighton & Leighton (1983), Lekagul & Round (1991), MacKinnon & Philipps (1993), Madoc (1976), Manger Cats-Kuennen (1961), van Marle & Voous (1988), Medway & Wells (1976), Meyer de Schauensee & Ripley (1940), Parrott & Andrew (1996), Poonswad (1993b), Reddish (1992), Riley (1938), Robson (2000a), Round (1985, 1988), Schneider (1945), Smythies (1986, 1999), Stattersfield & Capper (2000), Storer (1994a), Vowles & Vowles (1984), Wells (1999), Wetmore (1915), Wilkinson, Dutton & Sheldon (1991), van Zyl & Kemp (1998).







## PLATE 40

## Family BUCEROTIDAE (HORNBILLS) SPECIES ACCOUNTS

Genus *PENELOPIDES* Reichenbach, 1849

### 32. Sulawesi Tarictic Hornbill

*Penelopides exarhatus*

French: Calao des Célèbes

German: Celebeshornvogel

Spanish: Cálao Chico de Célebes

**Other common names:** Sulawesi(!)/Celebes(!) Hornbill/Dwarf-hornbill, Temminck's Hornbill

**Taxonomy.** *Buceros exarhatus* Temminck, 1823, Sulawesi.

Has been treated by some authors as conspecific with congeners. Two subspecies recognized.

**Subspecies and Distribution.**

*P. e. exarhatus* (Temminck, 1823) - N Sulawesi and Lembeh I.

*P. e. sanfordi* (Stresemann, 1932) - S Sulawesi and islands of Muna and Butung.

**Descriptive notes.** 45 cm; female 370 g. Small, black hornbill with green gloss on back. Male nominate race with white facial and throat plumage, but in life stained yellow, possibly by preen





oil; bill pale yellow, black at base of lower mandible, with low, ridged casque brown; bare skin around eye and on throat flesh-coloured. Female smaller, all-black facial skin and throat; casque and bill blacker than in male, with cream ridges across lower mandible and paler creamy tip. Juvenile like adult male, but smaller bill dull yellow, casque undeveloped; develops yellow facial colours from 80 days old, female acquires adult colours from c. 90-105 days. Race *sanfordi* differs mainly in having pale creamy yellow ridges across lower mandible. **Habitat.** Lowland primary forest, occasionally tall secondary forest, usually below 650 m but

sometimes up to 1100 m; family groups sometimes in more open habitats.

**Food and Feeding.** Diet mainly fruit (85%), of at least 34 plant species and 13 families; also some small animals, mainly invertebrates. Forages mostly through foliage below canopy. Reported to chase *Aceros cassidix*. Foraging territory when breeding 72-139 ha.

**Breeding.** Lays in Apr and Oct. Co-operative and territorial, in noisy groups of 2-10 birds, average 4, with adult helpers of both sexes. Nest in natural cavity or old woodpecker hole in large forest tree, including sites used by *Aceros cassidix*. Usually 2 eggs or chicks reported in wild, and nesting cycle 70-90 days; in captivity, 4 eggs, first laid 9 days after sealing in, rest at 2-day intervals, with incubation 28-30 days (reported as 16-19 days in wild) and fledging c. 50-60 days (55-70 in wild); female seals herself into nest, starts remex and rectrix moult before laying, emerges with chicks at end of nesting cycle; male delivers food to nest inmates by regurgitation.

**Movements.** Apparently sedentary and territorial.

**Status and Conservation.** Not globally threatened, CITES II. Locally common, although loss of lowland forest has fragmented its range, especially in S Sulawesi. Groups occupy home range of 1.5-2 km<sup>2</sup>, and some occur in reserves. Occurs in Dumonga-Bone National Park and in Lore Lindu National Park. Still hunted for food, and for keeping as pets.

**Bibliography.** Andrew (1992), Anon. (1995c), Baltzer (1990), van Bemmell & Voous (1951), Catterall (1997), Coates & Bishop (1997), Holmes (1979), Holmes & Phillips (1996), Holmes *et al.* (1993), Inskipp *et al.* (1996), Kemp (1976a, 1988), Mace & Azua (1997), MacKinnon (1979), O'Brien (1997), O'Brien & Kinnaird (1994, 1996b, 1996c), Poonswad (1993b), Rozendaal & Dekker (1989), Stresemann (1940), Wardill (1995), Wardill *et al.* (1999), Watling (1983), White & Bruce (1986), Whitten *et al.* (1987).

### 33. Visayan Tarictic Hornbill

#### *Penelopides panini*

**French:** Calao tarictic **German:** Visayan-Tariktikhornvogel **Spanish:** Calao Chico de Panay  
**Other common names:** Visayan Hornbill, Panay Tarictic Hornbill, Rufous-tailed Hornbill

**Taxonomy.** *Buceros Panini* Boddaert, 1783, Panay, Philippines.

Forms a superspecies with *P. manillae*, *P. affinis* and *P. mindorensis*, and all four formerly considered conspecific; *P. exarhatus* also treated as conspecific by some authors. Two subspecies recognized.

**Subspecies and Distribution.**

*P. p. ticaensis* Hachisuka, 1930 - Ticao, in NC Philippines.

*P. p. panini* (Boddaert, 1783) - Masbate, Panay, Sicoon, Pan de Azucar, Guimaras and Negros.

**Descriptive notes.** 45 cm. Small hornbill with prominently ridged bill. Male of nominate race yellowish-white and pale rufous, with black ear-coverts and cheeks, upperparts and wings black with bluish to olive sheen, tail-coverts above and below rufous, tail white to pale rufous with black tip; bill and small casque blackish-maroon, with reddish and yellowish ridges on both mandibles; bare skin around eye white, bare throat skin black. Female smaller, all black except tail, circumorbital and throat skin pale blue. Juvenile like adult of respective sex, but smaller brown bill. Race *ticaensis* larger, tail-coverts darker rufous, more rufous-washed



below.

**Habitat.** Primary evergreen forest, sometimes moving into secondary forest or visiting isolated fruiting trees; at up to 1050 m, though deforestation may have pushed it uphill to c. 1500 m.

**Food and Feeding.** Fruit; also insects, including beetles and ant alates, and earthworms. Forages below canopy and along forest edge.

**Breeding.** Lays in Mar-Apr. Breeds in pairs; possibly sometimes co-operative, in small groups of 2-3, less often 8, rarely up to 12 birds. Nest in natural hole in live or dead tree, height of 22 nests c. 2-19.5 m, mean 11 m; less often in rock hole; entrance sealed with wood flakes and food remains. Clutch 2-3 eggs; incubation period not recorded, possibly 30-35 days; male feeds female on nest by regurgitation; female moults while breeding, becomes temporarily flightless, emerges when oldest young fledges; nestling period 55-58 days; nesting cycle c. 95 days.

**Movements.** Apparently sedentary and territorial.

**Status and Conservation.** ENDANGERED, CITES II. Restricted-range species; present in Negros and Panay EBA. Was formerly common on larger islands. Now rare on Negros; still locally common in some hill forest remaining on Panay, where total population estimated at c. 750-1500 breeding pairs. Forest cover reduced by 70% or more on all islands; Masbate, Guimaras, Sicoon and Pan de Azucar almost totally deforested, and species likely to have been exterminated from those islands, with single records from Masbate and Pan de Azucar since 1990. Hunting remains rampant, accounting for both adults and young. Forest almost completely destroyed also on Ticao, where race *ticaensis* almost certainly now extinct. Present in Mt Canlaon Natural Park and North Negros Forest Reserve (Negros) and the proposed Central Panay Mountains National Park (Panay), in all of which the most immediate conservation action should probably be centred.

**Bibliography.** Anon. (1997a), Brooks *et al.* (1992), Collar, Crosby & Stattersfield (1994), Collar, Mallari & Tabaranza (1999), Curio, Hamman, Heubüschl & Lastimoza (1996), Delacour & Mayr (1946), Dickinson *et al.* (1991), Diesmos & Pedragosa (1995), Evans, Dutton & Brooks (1993), Gonzales & Rees (1988), Hamman & Curio (1998), Inskipp

*et al.* (1996), Kemp (1976a, 1988), Kennedy *et al.* (2000), Klop, Curio & Lastimoza (2000), Klop, Hahn *et al.* (2000), McGregor (1909-1910), duPont (1971, 1972), Poole (1995), Poonswad (1993b), Rabor (1977), Ripley & Rabor (1956), Robson (1994), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Worth *et al.* (1994).

### 34. Luzon Tarictic Hornbill

#### *Penelopides manillae*

**French:** Calao de Manille **German:** Luzon-Tariktikhornvogel **Spanish:** Calao Chico de Luzón  
**Other common names:** Luzon Hornbill

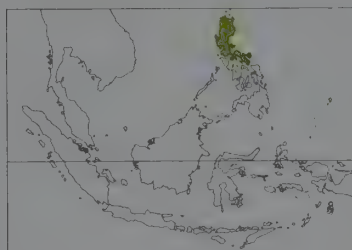
**Taxonomy.** *Buceros Manillae* Boddaert, 1783, Manila, Philippines.

Forms a superspecies with *P. panini*, *P. affinis* and *P. mindorensis*, and all four formerly considered conspecific; *P. exarhatus* also treated as conspecific by some authors. Original spelling of species name actually appears to be "manilloe", but appearance of diphthongs varies with original typescripts, and internal evidence from this same work clearly indicates author's intended name to have been "manillae". Two subspecies recognized.

**Subspecies and Distribution.**

*P. m. manillae* (Boddaert, 1783) - N Philippines, on Luzon, Marinduque, Catanduanes and adjacent islets.

*P. m. subniger* McGregor, 1910 - Polillo I and Patnanongan I.



**Descriptive notes.** 45 cm; male 395-479 g, female 470-475 g. Small hornbill with prominently ridged bill. Male nominate race creamy on head, neck and underparts, blackish ear-coverts, cheeks and throat, dark brown upperparts and wings, pale band across tail; bill and small casque brown and black, pale yellow to pink ridges on both mandibles, and pale tip; bare skin around eye and on throat pinkish. Female smaller, all brown to black, tailband brownier, circumorbital skin blue, throat skin edged blue. Juvenile resembles adult of respective sex, but smaller bill dull brown. Race *subniger* larger, black with metallic sheen above, broader pale

tailband.

**Habitat.** Primary evergreen dipterocarp forest in lowlands, riverine forest, and even single fruiting trees in grassland, at up to at least 900 m.

**Food and Feeding.** Figs and other fruits recorded, but probably also eats insects and other small animals. Occurs in small groups of up to 15 birds.

**Breeding.** Lays in Mar-Apr. Monogamous, some with immature helpers from previous season, and territorial. Nest in natural cavity in large forest tree, once 10 m up and with cavity diameter 20 cm. Clutch 3-4 eggs, rarely up to 6; in captivity, eggs laid 1-5 days apart, incubation 28-31 days, chick skin pink throughout development, male fed female in nest by regurgitation of fruit and animal food, female emerged about same time as chicks fledged, fledging 50-65 days.

**Movements.** Apparently sedentary and territorial.

**Status and Conservation.** Not globally threatened, CITES II. Previously considered Near-threatened. Restricted-range species; present in Luzon EBA. Was formerly common on Luzon, and appears still to be so in remaining primary forest, especially on Sierra Madre, but elsewhere recent declines reported; occurs in Quezon National Park, Luzon. Primary forest much reduced on other islands, including Polillo (estimated population 1000 birds) and Patnanongan (50 birds), where race *subniger* now exists mainly in secondary forest. Still hunted for food and trade on Polillo, mainly during breeding season, with up to 80 hornbills shot at a time.

**Bibliography.** Alday (1997), Azua & Azua (1988), Danielsen *et al.* (1994), Delacour & Mayr (1946), Dickinson *et al.* (1991), Frith & Douglas (1978), Gilliard (1950a), Gonzalez & Dans (1996), Goodman & Gonzales (1990), Inskipp *et al.* (1996), Jennings & Rundel (1976), Kemp (1976a, 1988), Lieras (1983), McGregor (1909-1910), duPont (1971), Poonswad (1993b), Poulsen (1995), Rabor (1977), Reinhard & Streliow (1998), Stattersfield *et al.* (1998), Worth *et al.* (1994).

### 35. Mindanao Tarictic Hornbill

#### *Penelopides affinis*

**French:** Calao de Mindanao **Spanish:** Calao Chico de Mindanao  
**German:** Mindanao-Tariktikhornvogel  
**Other common names:** Mindanao Hornbill

**Taxonomy.** *Penelopides affinis* Tweeddale, 1877, Mindanao, Philippines.

Forms a superspecies with *P. panini*, *P. manillae* and *P. mindorensis*, and all four formerly considered conspecific; *P. exarhatus* also treated as conspecific by some authors. Race *samarensis* sometimes treated as a separate species, but reasons for this unclear; further study needed. Three subspecies recognized.

**Subspecies and Distribution.**

*P. a. samarensis* Steere, 1890 - Samar, Calicoan, Leyte and Bohol, in EC Philippines.

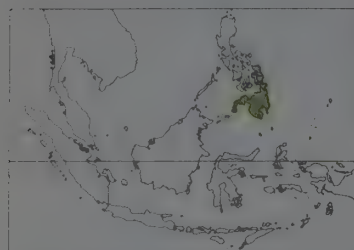
*P. a. affinis* Tweeddale, 1877 - Dinagat, Siargao and Mindanao.

*P. a. basilanicus* Steere, 1890 - Basilan.

**Descriptive notes.** 45 cm; male 456-554 g, female 394-514 g. Small hornbill with ridged lower mandible. Male of nominate race has much of plumage creamy, with black ear-coverts and throat, upperparts and wings black with metallic sheen, tail yellowish-brown with black base and tip; bill horn-coloured, blackish at base of upper mandible, lower with dark brown ridges, low casque dark brown; bare skin around eye and on throat bluish-white. Female averages somewhat smaller than male, all black except for central portion of tail, circumorbital and throat skin darker blue. Juvenile like adult male, but small brown bill. Race *samarensis* slightly larger, male uppertail-coverts light rufous, both sexes with less black on tail; *basilanicus* even less black on tail base, bill without dark base.

**Habitat.** Occupies primary evergreen forest, including edges of clearings and secondary forest, occurring up to c. 900 m.

**Food and Feeding.** Fruit, seeds, beetles and lizards recorded. Forages in middle and lower levels of forest, sometimes in groups of up to 12 birds.



**Breeding.** Little known. Birds in breeding condition in Apr-May. Usually recorded in pairs or small flocks. In captivity: both sexes sealed nest entrance, 3 eggs, incubation 25 days, chick retained pink skin throughout nestling period; fledging 47-54 days.

**Movements.** Apparently sedentary and territorial.

**Status and Conservation.** Not globally threatened. CITES II. Previously considered Near-threatened. Restricted-range species: present in Mindanao and the Eastern Visayas EBA. Still common in remaining primary forest on Samar, and probably Leyte. Occurs in Rajah

Sikatuna National Park (Bohol). Large tracts of forest remain on Mindanao, but other islands more deforested, and Dinagat almost without forest. Hunted for food.

**Bibliography.** Brooks *et al.* (1996), Buay (1991), Delacour & Mayr (1946), Dickinson *et al.* (1991), Evans, Dutson & Brooks (1993), Forshaw & Cooper (1994), Inskipp *et al.* (1996), Kemp (1976a, 1988), Lint & Stott (1948), Parkes (1971), duPont (1971), duPont & Rabor (1973a), Potter (1953), Rabor (1977), Rand & Rabor (1960), Stattersfield *et al.* (1998), Stott (1947), Witmer (1988a), Worth *et al.* (1994).

### 36. Mindoro Tarictic Hornbill

#### *Penelopides mindorensis*

**French:** Calao de Mindoro

**Spanish:** Cálao Chico de Mindoro

**German:** Mindoro-Tariktikhornvogel

**Other common names:** Mindoro Hornbill

**Taxonomy.** *Penelopides Mindorensis* Steere, 1890, Mindoro, Philippines.

Forms a superspecies with *P. panini*, *P. manillae* and *P. affinis*, and all four formerly considered conspecific; *P. exarhatus* also treated as conspecific by some authors. Monotypic.

**Distribution.** Mindoro (NC Philippines).



**Descriptive notes.** 45 cm. Small hornbill, black and yellowish-white with large white to beige to rufous patch on black tail. Male has black ear-coverts and throat; bill dark brown to black with yellow stripes and tip, low casque; bare skin around eye and on throat flesh-pink. Female like male but smaller, facial and throat skin blue; the only species of genus in which female is not almost entirely black. Juvenile similar to adult, but smaller bill without stripes.

**Habitat.** Inhabits primary evergreen forest, extending to forest edge, secondary forest, and even isolated fruiting trees; generally

found in lowlands, rarely up to 1000 m.

**Food and Feeding.** Fruits recorded in diet, mainly figs; possibly also takes some insects. Usually seen in pairs; occasionally in flocks, of up to 20 birds.

**Breeding.** Female in breeding condition in May. No other information.

**Movements.** Probably sedentary and territorial.

**Status and Conservation.** ENDANGERED. CITES II. Restricted-range species: present in Mindoro EBA. Formerly abundant and apparently still quite common in 1970's, but the single island on which it occurs has lost c. 80% of its original forest habitat; this makes the area of remaining habitat very vulnerable, and size of the remaining population is likely to be very small. Recorded at only five localities since 1990, with local reports that it may still survive at another seven or more sites. Main threat is continued destruction of already heavily fragmented remaining patches of forest; hunting also continues at unsustainable levels. Comprehensive surveys urgently required; a network of strictly protected reserves should be set up before it is too late for this species and other sympatric endemics.

**Bibliography.** Anon. (1997a), Brooks, Dutson *et al.* (1995), Collar, Crosby & Stattersfield (1994), Collar, Mallari & Tabaranza (1999), Delacour & Mayr (1946), Dickinson *et al.* (1991), Diesmos & Pedragosa (1995), Dutson *et al.* (1992), Evans, Dutson & Brooks (1993), Inskipp *et al.* (1996), Kemp (1976a, 1988), McGregor (1905, 1909-1910), duPont (1971), Rabor (1977), Ripley & Rabor (1958), Robson (1993), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Worth *et al.* (1994).







PLATE 41

inches 9  
cm 23



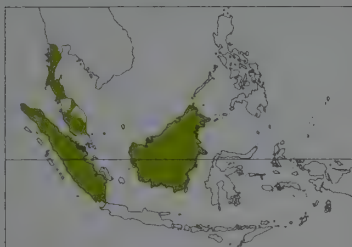
# Genus *BERENICORNIS* Bonaparte, 1850

## 37. White-crowned Hornbill

### *Berenicornis comatus*

**French:** Calao coiffé **German:** Langschopf-Hornvogel **Spanish:** Calao Crestiblanco  
**Other common names:** White-crested/Long-crested Hornbill

**Taxonomy.** *Buceros comatus* Raffles, 1822, Sumatra. Often placed in genus *Aceros*. Thought by some to be closely related to *Tropicranus albocristatus*, which is sometimes included in present genus, but plumage and voice markedly distinct within context of family. Monotypic.  
**Distribution.** S Myanmar and S Thailand, Peninsular Malaysia, Sumatra and Borneo; recently recorded in SW Cambodia.



**Descriptive notes.** 75-80 cm; young male 1250-1360 g, female 1470 g. Large hornbill with tall spiky crest, black back, wings and thighs; long, graduated white tail and white tips to wing feathers distinctive. Male has white head, crest, neck and underparts; black bill with yellowish wash at base, low casque blackish; bare skin around eye and on throat blue. Female smaller, also white crest, but face, neck and whole body black. Juvenile all black, but for broad white tip to tail, white tips to head, neck and breast feathers giving overall grey appearance, bill dull yellow, bare skin greyish.

**Habitat.** Inhabits primary lowland evergreen

forest; extends into adjacent plantations and dense secondary growth; usually below 900 m, but up to 1680 m.

**Food and Feeding.** Large proportion of animal food, including insects, snakes, lizards and small birds; also various fruits, mainly lipid-rich drupes and capsules, with some figs. Forages in dense tangled growth, usually at lower levels or on ground; spends much time digging among bark, stems and debris for animal food.

**Breeding.** Little known. Lays aseasonally, in Jan, Mar, Jun, Oct and Dec. Co-operative in groups of 3-8 birds, which keep in contact with mellow cooing notes; only dominant female breeds, and chases off other females in group. Probably 2 eggs, but usually only single chick raised; no information on incubation and fledging periods.

**Movements.** Apparently sedentary and territorial.

**Status and Conservation.** Not globally threatened. CITES II. Currently considered Near-threatened. Generally uncommon, although tends to be inconspicuous and easily overlooked; in places survives in small forest patches with home range of 1-10 km<sup>2</sup>. Very few individuals remain in Thailand, where species now endangered, and rare in Malay Peninsula; population recently discovered in Cambodia. Recorded from several protected areas, e.g. Gunung Leuser and Way Kambas National Parks (Sumatra), but rather rarely observed throughout range.

**Bibliography.** Andrew (1992), Chak Sokhachevich (1998), Davison (1995), Dunselman (1937), Frith & Douglas (1978), Holmes (1996), Holmes *et al.* (1993), Inskipp *et al.* (1996), Jeyarajasingam & Pearson (1999), Johns (1987, 1988), Kemp (1979, 1988), Leighton (1982, 1986), Leighton & Leighton (1983), Lekagul & Round (1991), MacKinnon & Philipps (1993), van Marle & Voous (1988), Medway & Wells (1976), Ng Beechoo (1998), Parrott & Andrew (1996), Poonswad (1993b), Riley (1938), Robson (2000a), Round (1985), Smythies (1986, 1999), Stattersfield & Capper (2000), Vowles & Vowles (1984), Wells (1999), Wilkinson, Dutton & Sheldon (1991), van Zyl & Kemp (1998).

# Genus *ACEROS* J. E. Gray, 1844

## 38. Rufous-necked Hornbill

### *Aceros nipalensis*

**French:** Calao à cou roux **German:** Nepalhornvogel **Spanish:** Calao del Nepal

**Taxonomy.** *Buceros Nipalensis* Hodgson, 1829, Kathmandu, Nepal. Sometimes considered distinct and treated as sole member of genus, with all of current congeners then placed in *Rhyticeros*. Monotypic.

**Distribution.** Bhutan and NE India E to S China (W & S Yunnan), and S to W & S Myanmar, N & W Thailand, N Laos and NW Vietnam.



**Descriptive notes.** 90-100 cm; male 2500 g, female 2270 g. Very large hornbill; has rather pale yellow bill with black stripes. Male has rufous head, neck and underparts, glossy black upperparts and wings, broad white tips of wings, black tail with white distal half; bare skin around eye blue; inflatable bare throat skin red, enhanced by violet-blue patch at base of lower mandible and under chin. Female smaller than male; rufous parts of plumage replaced by black, circumorbital skin duller blue, throat skin more violet-blue. Juvenile somewhat similar to adult male, but bill smaller without dark stripes.

**Habitat.** Dense evergreen and deciduous hill forest, mainly along ridges and in mountains, at 150-2200 m, usually within range 600-1800 m.

**Food and Feeding.** Mainly fruits, including figs and mangoes. Forages in canopy, only rarely descending to ground for fallen items. Usually in pairs or in small family groups of 4-5, occasionally more.

**Breeding.** Little known. Lays in Jan-Jun; pair engaged in courtship display, mid-Apr, in Bhutan. Nest in natural hole 10-30 m up in tall forest tree; female seals nest with droppings and food remains. Clutch 1-2 eggs; female remains sealed in nest for c. 3 months, emerges when chick fledges; incubation and fledging periods not documented.

**Movements.** Probably sedentary; only short local movements, some of which may be seasonal, in response to fruiting of main food trees.

**Status and Conservation.** VULNERABLE. CITES II. Despite widespread distribution, species has disappeared or declined over much of range; now extinct in Nepal and NW Thailand, very rare in China, and only 1-3 birds/100 km<sup>2</sup> in India; still locally common in Bhutan; local but regular in Myanmar, CW Thailand, Laos and Vietnam. Main causes of decline are habitat loss and hunting; dependence on large trees for nesting, together with requirement of large home range, make species particularly vulnerable to all forms of forest destruction. Widely hunted by hill tribes, and found only in taller stands of hill and montane forest trees; killed for food, but also for casque; young sometimes captured for pet trade. Generally small but significant populations occur in protected areas, e.g. Namdapha National Park (India), Thrumshing La National Park (Bhutan), Xishuangbanna Nature Reserve (China), Um Phang and Maewong National Parks and Huai Kha Khaeng Wildlife Sanctuary (Thailand), and Nakai-Nam Theun National Biodiversity Conservation Area (Laos).

**Bibliography.** Ali (1996), Ali & Ripley (1983), Ali *et al.* (1996), Baker (1934a), Bangs & Van Tyne (1931), Bishop (1999a, 1999b), Cheng Tsohsin (1973), Chimehome *et al.* (1998), Collar & Andrew (1988), Collar *et al.* (1994), Davidson (1998), Deignan (1945), Duckworth *et al.* (1999), Evans & Timmins (1998), Gammie (1874), Ghosh (1994), Grimmett *et al.* (1998), Harvey (1990), Inskipp & Inskipp (1991), Inskipp, Inskipp & Grimmett (1999), Inskipp, Inskipp & Sherub (2000), Kemp (1979, 1988), Lan Yang & Xianji Wen (1993), Lekagul & Round (1991), MacKinnon & Philipps (2000), Poonswad (1993b), Poonswad, Chimehome *et al.* (1998), Riley (1938), Ripley (1982), Robson (2000a), Round (1985, 1988), Smythies (1986), Stattersfield & Capper (2000), Thewlis *et al.* (1998), Tickell (1864), Tikader (1983), Tynstra *et al.* (1997), Zhao Zhengjie (1995).

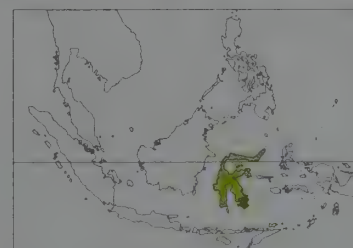
## 39. Knobbed Hornbill

### *Aceros cassidix*

**French:** Calao à cimier **German:** Helmhornvogel **Spanish:** Calao Grande de Célebes  
**Other common names:** Butung/Red-knobbed Hornbill, Sulawesi(!)/Celebes(!) Hornbill, Wrinkled Hornbill

**Taxonomy.** *Buceros cassidix* Temminck, 1823, Sulawesi. Sometimes placed in genus *Rhyticeros*. May form a superspecies with *A. corrugatus*, *A. leucocephalus* and *A. waldeni*. Monotypic.

**Distribution.** Sulawesi, and offshore islands of Lembeh, Togian Is, Muna and Butung.



**Descriptive notes.** 70-80 cm; male 2360-2500 g. Large hornbill with white tail and high casque. Male crown and nape deep rufous, head sides and neck paler rufous to creamy, body and wings black; bill yellow, ridged base orange and brown, wrinkled casque red; bare skin around eye pale blue; extensive bare throat skin light and dark blue and black. Female smaller, with head and neck black, smaller casque yellow, throat skin with smaller black band. Juvenile like adult male, but small casqueless bill plain yellow.

**Habitat.** Evergreen forest at up to 1800 m, especially in lowlands below 1100 m, where ex-

tends into patches of secondary forest, woodland and plantations to forage.

**Food and Feeding.** Mainly fruit; also animal food, including insects, and bird eggs and nestlings, but only 1% of diet. Fruits of at least 35 plant species in 13 genera recorded during non-breeding season, especially 17 fig species, which form 85% of diet; 52 species when breeding, with figs 60-82%. Forages mainly in canopy, even plucking off fruits in flight; also digs in soft wood. Chases off other birds and primates at feeding sites.

**Breeding.** Lays in Jun-Sept; season probably triggered by end of rains, so that fruiting peaks when chick fledges. Nests in pairs. Nest in natural hole 13-53 m up in tall forest tree, at least 15 tree species recorded, 50-62% of holes reused in successive seasons; female seals entrance with own droppings. Clutch 2-3 eggs in captivity, re-laying after failure; in wild, only 1 chick usually raised, rarely 2; pre-laying period in nest 5-8 days; incubation c. 32-35 days; chick hatches with pink skin that soon turns black; male feeds female and chicks, regurgitating food items at nest; female emerges after 58-140 days, assists male with brood-feeding, provides on average 14% of food for chick; nestling period c. 100 days, mean total nesting cycle 139 days. Young fledged from 80% of nesting attempts.

**Movements.** Wanders locally during non-breeding season in search of food, especially large red figs; moves in flocks of up to 50 birds, covering up to 30-60 km<sup>2</sup> daily.

**Status and Conservation.** Not globally threatened. CITES II. Locally very common, especially in areas with many fig trees, with nesting densities reaching 10 pairs/km<sup>2</sup>, non-breeding densities of 51 birds/km<sup>2</sup>, and flocks of 50. Widespread, but 60% of lowlands have been deforested, and removal of forest is an ongoing process, especially on smaller islands. Common in several small reserves, and occurs in Dumoga-Bone National Park and Lore Lindu National Park. Distribution, however, increasingly more patchy, and this exacerbated by further habitat loss, fires, gold-mining and continued hunting; following exceptional fires in 1997, fieldwork showed significant drop in breeding success and population recruitment in subsequent years. Important disperser of seeds of Meliaceae and Myristicaceae forest trees.

**Bibliography.** Andrew (1992), Baltzer (1990), van Bommel & Voous (1951), Cahill & Walker (2000), Catterall (1997), Coates & Bishop (1997), Holmes (1979), Holmes *et al.* (1993), Inskipp *et al.* (1996), Kemp (1979, 1988), Kinnaird (1998), Kinnaird & O'Brien (1993, 1997, 1998, 1999), Kinnaird, O'Brien & Sinclair (1998), Kinnaird, O'Brien & Suryadi (1995, 1996), Michi (1992), O'Brien & Kinnaird (1996b, 1996c), Poonswad (1993b), Primm (1996), de Roy (1996), Rozendaal & Dekker (1989), Scheres & Alba (1997), Stresemann (1940), Suryadi, Kinnaird

& O'Brien (1998), Suryadi, Kinnaird, O'Brien, Supriatna & Somadikarta (1994, 1996), Wardill (1995), Wardill *et al.* (1999), Wailing (1983), White & Bruce (1986), Yustandra *et al.* (1995).

## 40. Wrinkled Hornbill

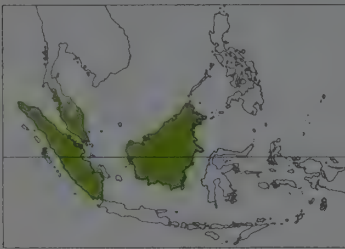
### *Aceros corrugatus*

**French:** Calao à casque rouge **German:** Runzelhornvogel **Spanish:** Cálao Arrugado  
**Other common names:** Sunda Wrinkled Hornbill

**Taxonomy.** *Buceros corrugatus* Temminck, 1832, Borneo.

Sometimes placed in genus *Rhyticeros*. May form a superspecies with *A. cassidix*, *A. leucocephalus* and *A. waldeni*. Has in past sometimes been treated as conspecific with *A. leucocephalus*, but the two show clear morphological differences. Birds from Asian mainland S to Sumatra and nearby islands have sometimes been separated as race *rugosus* (or *megistus*), on basis of larger size. Monotypic.

**Distribution.** S Thailand, Peninsular Malaysia, Sumatra (including islands of Rupat and Payong), Batu Is and Borneo; recently recorded in SW Cambodia.



**Descriptive notes.** 65–70 cm; male 1590 g. Large hornbill with pale tail. Male crown, hindneck, body and wings black; sides of head, neck and upper breast white, tail white with black base; white areas often stained yellow-ochre to red-brown with green oil; bill yellow, base red, lower mandible ridged at base; wrinkled casque red; bare skin around eye blue, inflatable throat skin yellowish. Female smaller, head to breast black, bill and smaller casque yellow, throat skin blue. Juvenile resembles adult male, but bill small, casqueless and pale yellow.

**Habitat.** Lowland evergreen forest, including

coastal swamp-forest; extends into selectively logged forest, but not secondary forest; rarely above 30 m, but up to 250 m.

**Food and Feeding.** Variety of lipid-rich drupes and some figs; also some animal items when available. Forages mainly in large emergent trees, searching among canopy foliage or plucking off items in flight. Usually in pairs, but sometimes in small flocks of up to 30 birds.

**Breeding.** Little known in wild. Lays in Jan–May. Nest in natural cavity in large tree; female seals nest with droppings and food remains. In captivity, 2–3 eggs, rarely 4, after pre-laying period 4–6 days (rarely, 30 days); re-lays after failure; incubation 29 days; chick hatches with pink skin that turns dark purple-black after c. 10 days; male feeds female in nest by regurgitation; female leaves nest when chicks fledge; fledging 65–73 days; whole cycle 111–124 days.

**Movements.** Extensive local movements to track availability of fruiting trees and attend communal roosts; even crosses open sea.

**Status and Conservation.** Not globally threatened. CITES II. Currently considered Near-threatened. Previously classed as Vulnerable. Always uncommon, but now rare in many areas of Malay Peninsula; may be extinct in Thailand; still reasonably common in parts of Borneo (Kalimantan), in flocks of up to 12, but declining rapidly; locally still quite common in Sumatra, e.g. in Riau, where several flocks seen in 1990, including one numbering 24 individuals. Occurs in Gunung Leuser and Way Kambas National Parks (Sumatra) and Danum Valley Conservation Area (Borneo). One of the most habitat-specific of Asian hornbills, requiring large tracts of tall lowland forest and not readily entering degraded habitat; this same habitat is the one most altered by human influences throughout the species' range.

**Bibliography.** Anon. (1995c), Chak Sokhachicheaboth (1998), Collar & Andrew (1988), Collar *et al.* (1994), Daniels & Heegaard (1995), Duckett (1985), Holmes (1996, 1997), Holmes *et al.* (1993), Inskipp *et al.* (1996), Jeyarajasingam & Pearson (1999), Johns (1987, 1988), Kemp (1979, 1988), Kemp & Kemp (1975a), Lambert (1989), Leighton (1986), Leighton & Leighton (1983), Lekagul & Round (1991), Low (1994a, 1994b), Luttenberg & Bisselink (1999), MacKinnon & Phillips (1993), van Marle & Voous (1988), Medway & Wells (1976), Petit (1997), Primm (1996), Reilly (1997), Riley (1938), Robson (2000a), Round (1985, 1988), de Ruiter (1994), Scheres & Alba (1997), Sigler & Myers (1992), Smythies (1999), Stattersfield & Capper (2000), Summers (1997), Wells (1990, 1999), Wilkinson, Dutson & Sheldon (1991), Wilkinson, McLeod *et al.* (1996), Wong Hongmun & Khin Maynyunt (1998).

## 41. Writhed Hornbill

### *Aceros leucocephalus*

**French:** Calao de Vieillot **German:** Mindanaohornvogel **Spanish:** Cálao Grande de Mindanao  
**Other common names:** Writhe-billed(!)/White-headed Hornbill, Wrinkled(!)/Mindanao Wrinkled Hornbill

**Taxonomy.** *Buceros leucocephalus* Vieillot, 1816, Moluccas; error = Mindanao, Philippines.

Sometimes placed in genus *Rhyticeros*. May form a superspecies with *A. cassidix*, *A. corrugatus* and *A. waldeni*. Often considered conspecific with *A. waldeni*, but differs in plumage and bare-part colours, and in degree of sexual dimorphism in colour of facial skin. In the past, was sometimes treated as conspecific with *A. corrugatus*, but differs markedly in several aspects of morphology. Monotypic.

**Distribution.** Dinagat, Siargao, Camiguin and Mindanao (S Philippines).

**Descriptive notes.** 60–65 cm; male 1012–1295 g. Medium-sized black hornbill with black-tipped white tail. Male has crown and hindneck dark brown, face and neck to upper breast white, stained creamy by green oil; bill red, base of lower mandible with blue-black grooves, wrinkled casque red; bare skin around eye and on throat deep orangey-red. Female smaller, head to breast all black, facial skin paler, more orange. Juvenile resembles adult male, but bill small, unridged, paler, no casque.



**Habitat.** Primary evergreen forest in lowlands, mainly below 500 m, but up to 1100 m.

**Food and Feeding.** Mainly fruit, and some insects. Feeds in canopy of tall forest trees; sometimes hawks insects in flight. Forages over wide areas, often feeding and roosting in company of *Buceros hydrocorax*. Usually in pairs, rarely in flocks of as many as 37 birds.

**Breeding.** Almost unknown in wild. Sealed nest recorded in Mar; fledged young in Jan. In captivity, 2 eggs, female emerges at same time as chicks fledge, total nesting cycle 92 days, re-lays after failure.

**Movements.** Ranges widely in search of fruiting trees and communal roosts.

**Status and Conservation.** Not globally threatened. CITES II. Currently considered Near-threatened. Restricted-range species: present in Mindanao and the Eastern Visayas EBA. Previously considered Endangered. Used to be common on Mindanao but now apparently rare in general, even in larger forest reserves on Mt Apo, though still locally quite common in places. Forest now much reduced on smaller islands, where species probably either rare or extinct. Its requirement for primary forest, along with its wide-ranging habits and low overall density, render it vulnerable; also subjected to pressure from hunting and trapping for wild bird trade.

**Bibliography.** Anon. (1997a), Brooks *et al.* (1992), Collar, Crosby & Stattersfield (1994), Collar, Mallari & Tabaranza (1999), Delacour & Mayr (1946), Dickinson *et al.* (1991), Evans, Dutson & Brooks (1993), Gonzales & Rees (1988), Inskipp *et al.* (1996), Johnson (1989), Jung (1991), Kemp (1979, 1988), Kennedy *et al.* (2000), Lint & Stott (1948), McGregor (1909), Myers (2000), duPont (1971), duPont & Rabor (1973a), Poonswad (1993b), Primm (1996), Rand & Rabor (1960), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Stott (1947), Witmer (1988a), Worth *et al.* (1994).

## 42. Rufous-headed Hornbill

### *Aceros waldeni*

**French:** Calao de Walden **German:** Waldenhornvogel **Spanish:** Cálao Grande de Panay  
**Other common names:** Writhe-billed Hornbill(!), Panay/Visayan Wrinkled Hornbill

**Taxonomy.** *Craniorrhinus* [sic] *waldeni* Sharpe, 1877, Panay, Philippines.

Sometimes placed in genus *Rhyticeros*. May form a superspecies with *A. cassidix*, *A. corrugatus* and *A. leucocephalus*. Often considered conspecific with *A. leucocephalus*, but differs in plumage, bare parts, and in degree of sexual dimorphism in colour of facial skin. Monotypic.

**Distribution.** Panay, Guimaras and Negros (C Philippines).



**Descriptive notes.** 60–65 cm. Medium-sized black hornbill with broadly black-tipped white tail that becomes stained rufous with green oil. Male crown and hindneck dark brown, head and neck and upper breast rufous; bill orange-red, base of lower mandible ridged, high wrinkled casque red and orange; bare skin around eye and on throat saffron-yellow; eyes deep red. Female smaller, head to breast black, blue or green tinge to less extensive facial skin, eyes browner. Juvenile similar to adult male, but bill smaller, paler and casqueless, facial skin white or pinkish, eyes pale grey.

**Habitat.** Inhabits evergreen forest with closed

canopy, but will also use selectively logged forest, and even recorded at times at large trees in clearings; occurs from coast up to 950 m on Negros, to 1200 m on Panay. Seems to require larger trees for nesting than does partially sympatric *Penelopides panini*.

**Food and Feeding.** Mainly fruit, including figs. Usually encountered in only small groups of up to 4 birds, rarely 25–30.

**Breeding.** Probably lays in Mar; chicks collected from nests in May–Jul. Nest in natural cavity in large *Shorea polysperma* tree, or in old woodpecker hole, 2 nests each 17 m above ground; both sexes seal entrance. Aggressive towards *Penelopides panini* near nest. Clutch 2 eggs, rarely 3; no other information.

**Movements.** Probably sedentary, except for local movements in search of food.

**Status and Conservation.** CRITICAL. CITES II. Restricted-range species: present in Negros and Panay EBA. Very few documented records since first discovered in 1870's, and hardly any for first 80 years thereafter. Fieldwork on Panay in 1990's found density of 0.2–0.3 nests/km<sup>2</sup>, and maximum of 60–100 pairs estimated; recently recorded at three sites on Negros, including breeding birds; forest habitat virtually eliminated on Guimaras, and species presumed extinct there. Lowland forest on Panay and, especially, on Negros much reduced; although it seems to prefer hill forest, which has been slightly less affected, species is now very rare and local. Still hunted, and up to 25% of total population of NW Panay shot on a single day in 1997; nests robbed for food and trade, and, especially on Panay, for local exhibition. Appears to be on brink of extinction, unless effective conservation measures taken; increase in public awareness of the problems facing this species are essential for its survival. Present in Mt Canlaon Natural Park and North Negros Forest Reserve (Negros) and the proposed Central Panay Mountains National Park (Panay), in all of which the most immediate conservation action should probably be centred.

**Bibliography.** Anon. (1997a), Brooks *et al.* (1992), Collar, Crosby & Stattersfield (1994), Collar, Mallari & Tabaranza (1999), Crosby (1997), Curio, Hamman & Lastimosa (1996), Delacour & Mayr (1946), Dickinson *et al.* (1991), Diesmos & Pedragosa (1995), Evans, Dutson & Brooks (1993), Hamman & Curio (1998), Heaney & Regalado (1998), Inskipp *et al.* (1996), Kauth *et al.* (1998), Kemp (1979, 1988), Kennedy *et al.* (2000), Klop, Curio & Lastimosa (2000), duPont (1971), Poole (1995), Robson (1994b), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Worth *et al.* (1994).





43

S Moluccan birds

E New Guinean bird

E Solomon bird

44

45

46

47

PLATE 42

inches 7  
cm 18



# Genus *RHYTICEROS* Reichenbach, 1849

## 43. Papuan Hornbill

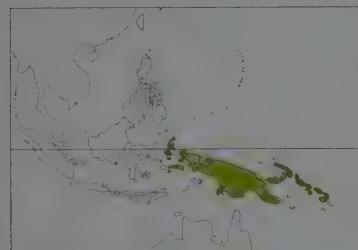
### *Rhyticeros plicatus*

**French:** Calao papou **German:** Papuahornvogel **Spanish:** Cálao Papú  
**Other common names:** Blyth's(!)/New Guinea/Plicated Hornbill, Papuan Wreathed Hornbill

**Taxonomy.** *Buceros plicatus* J. R. Forster, 1781, Seram.

Genus sometimes merged with *Aceros*. Has been thought to form a superspecies with *R. subruficollis*, and in past these two frequently considered conspecific. Has also been deemed possibly conspecific with *R. narcondami*, but differs significantly in size and in details of bill colour. Several geographical races have been described, from N Moluccas to C New Guinea (*ruficollis*), E New Guinea (*jungei*), Bismarck Archipelago (*dampieri*), W Solomons (*harterti*), and E Solomons (*mendanae*), leaving nominate race for populations of S Moluccas only; however, variation appears to be largely clinal, with overlap in size and colours, and boundaries difficult to define. Monotypic.

**Distribution.** N Moluccas, Seram and Ambon through New Guinea and adjacent islands to Bismarck Archipelago, and E to Solomon Is (Buka, Bougainville, Shortland, Choiseul, Santa Isabel, Guadalcanal and Malaita).



**Descriptive notes.** 65-85 cm; male 1190-2000 g, female 1500-2000 g. Medium-sized to large black hornbill with short white tail. Male head and neck rufous, varying W to E from deep rufous to golden-rufous to golden-yellow; bill pale yellow, base dark brown; low wreathed casque yellow and brown; bare skin around eye and on throat bluish-white; eyes and eyerings red. Female smaller than male, with head and neck all black; bill with less brown around base, eye duller. Juvenile similar to male, but bill smaller, no casque.

**Habitat.** Evergreen primary and secondary forest, also extending to deciduous riverine woodland and swamp-forest; occurs at elevations up to 1500 m, rarely up to 1800 m.

**Food and Feeding.** Feeds mainly on fruits, both figs and those of other tree genera; also takes animal food, including crabs taken on beaches, and bee honeycomb. Usually recorded in pairs or in small flocks.

**Breeding.** Little known in wild. Probably lays from about Aug-Oct in W to Jan-May in E. Nest in natural hole in forest tree. Clutch 1-2 eggs; male feeds female in nest by regurgitation; in captivity, whole nesting cycle 125 days.

**Movements.** No regular movements reported, but in most areas gathers at times at communal roosts of hundreds of birds, which make extensive local movements in search of food. Occasionally wanders to islands outside regular breeding range.

**Status and Conservation.** Not globally threatened. CITES II. Common in many areas of its wide range; even abundant on larger islands, with counts of 250 along 20 km of river in Irian Jaya; uncommon on Obi. Extensive tracts of forest with large trees for nesting still available overall, but locally and on smaller islands declining, and still widely hunted. Broad habitat tolerance and absence of any sympatric hornbills favour its survival.

**Bibliography.** Alday (1997), Andrew (1992), Boehler *et al.* (1986), Bishop (1992), Blaher (1990), Coates (1985), Coates & Bishop (1997), Coupe (1967), Diamond (1972), Doughty *et al.* (1999), Elbel (1977), Euing (1995), Finch (1981e), Finch & McKean (1987), Gilliard & LeCroy (1966, 1967a), Greenway (1966), Gregory (1995a, 1995b), Hadden (1981), Holmes *et al.* (1993), Hoogerwerf (1964), Inskipp *et al.* (1996), Isherwood *et al.* (1997), Jennings & Rundel (1976), Kemp (1979, 1988), King *et al.* (1996), LeCroy & Peckover (1983), Linsley (1995), Mangold (2000), Mayr & Rand (1937), Mees (1965, 1982), O'Brien & Kinnaird (1996b), Peckover & Filewood (1976), Poonswad (1993b), Rand & Gilliard (1967), Ripley (1964), Scheres & Alba (1997), Schmid (1993), Schodde & Hitchcock (1968), White & Bruce (1986), Widodo *et al.* (1998), Worth *et al.* (1994).

## 44. Narcondam Hornbill

### *Rhyticeros narcondami*

**French:** Calao de Narcondam **German:** Narcondamhornvogel **Spanish:** Cálao de la Narcondam  
**Other common names:** Narcondam Wreathed Hornbill

**Taxonomy.** *Rhyticeros narcondami* Hume, 1873, Narcondam, Andaman Islands.

Genus sometimes merged with *Aceros*. In past, species was considered possibly conspecific with *R. plicatus*, but geographical isolation, together with notable difference in size and lesser differences in bill colour, supports their treatment as two separate species. Monotypic.

**Distribution.** Narcondam I, in NE Andamans.



**Descriptive notes.** 45-50 cm; male 700-750 g, female 600-750 g. Small, black hornbill with short white tail; appearance is of a miniature version of *R. plicatus*. Male has head and neck rufous, with shaggy crest; bill yellowish-white, base dark crimson; low wreathed casque yellow and dark brown; bare skin around eye blue, on throat bluish-white; eyes dark orange-brown, eyerings red. Female smaller, head and neck all black, eyes browner. Juvenile similar to male, but bill smaller, no casque.

**Habitat.** Occupies relatively open, mixed evergreen and deciduous forest, and dense bush; occurs from coast up to island's summit, at 750 m.

**Food and Feeding.** Mainly fruit, of at least 9 species, with principal component figs; no animal food recorded. Congregates at fruiting trees in groups of up to 50.

**Breeding.** Lays in Feb-Apr. Breeds in pairs; active nests sometimes only 23 m apart. Nest in natural cavity 2.4-15.2 m up in tree, at least 3 tree species known to be used; female seals nest entrance. Clutch 2 eggs, laid c. 10 days apart; female fed by male by regurgitation, 10-93 items per visit; female may start moult before nesting, then drops remaining old remiges and rectrices soon after laying; no information on incubation and fledging periods.

**Movements.** Sedentary.

**Status and Conservation.** VULNERABLE. CITES II. Total range only 6820 ha, not all of which is prime habitat. Population always small, previously reckoned at only 200 individuals, but might be at least double that number; latest estimate is of c. 295-320 individuals, including c. 68-85 breeding pairs. Large nest trees are vulnerable to cyclones. Most immediate threat is from habitat deterioration; police contingent stationed on the island in 1969, growing some crops and running goats, which now number c. 400 and which eliminate most of undergrowth and seedlings; feral cats now abundant, though their impact on present species remains unknown; small but potentially significant numbers of live trees felled each year for various human uses; hunting probably accounts for c. 25-40 birds each year, though such losses probably sustainable due to apparently adequate recruitment. Whole island is a wildlife sanctuary, and hunting has been expressly outlawed; strict conservation measures essential for species' long-term survival; susceptibility of the highly localized population to natural disasters has caused some to suggest possible advisability of establishing a second population on some nearby island, although such procedures can involve considerable risks in ecological terms; top priorities should be removal of alien species, especially goats, and urgent measures to promote recovery of natural regeneration processes of forest.

**Bibliography.** Abdulah (1971, 1974b), Ali & Ripley (1983), Baker (1934a), Collar & Andrew (1988), Collar *et al.* (1994), Cory (1902), Frith & Douglas (1978), Ghosh (1994), Green & Hiron (1991), Grimmett *et al.* (1998), Hussain (1984, 1991), Inskipp *et al.* (1996), Kazmierczak (2000), Kemp (1979, 1988), Osmaston (1905), Poonswad (1993b), Ripley (1982), St John (1988), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Tikader (1983, 1984), Worth *et al.* (1994).

## 45. Plain-pouched Hornbill

### *Rhyticeros subruficollis*

**French:** Calao à gorge claire **German:** Blythhornvogel **Spanish:** Cálao Gorgiclaro  
**Other common names:** Plain-pouched Wreathed Hornbill, Blyth's(!)/Blyth's Wreathed/Burmese/Tenasserim Hornbill

**Taxonomy.** *Buceros subruficollis* Blyth, 1843, Tenasserim.

Genus sometimes merged with *Aceros*. Sometimes thought to form a superspecies with *R. plicatus*. Has in past been considered conspecific with *R. plicatus* or with *R. undulatus*, but differs from both in size, bill morphology and bare-part colours; evidence from feather lice (*Mallophaga*) inconclusive, with different louse genera pointing towards potential relationships with one or other of the above species. Monotypic.

**Distribution.** S Myanmar and W & S Thailand, and recently confirmed N Peninsular Malaysia; reports from farther S (to Sumatra) unconfirmed.



**Descriptive notes.** 65-70 cm; male 1815-2270 g. Large, black hornbill with short white tail. Male has crown and nape dark rufous-brown, sides of head down to upper breast creamy white; bill pale yellow, base red-brown; low wreathed casque yellowish-white with red-brown; bare skin around eye purplish-red, extensive inflatable throat skin yellow. Distinguished from very similar *R. undulatus* by smaller size, dark red bill base, lack of ridges on mandibles, no dark bar on throat sac. Female smaller than male, head to breast all black, throat sac blue. Juvenile similar to adult male, but small bill, no casque.

**Habitat.** Evergreen and mixed deciduous hill forest, especially along river valleys; typically in lowlands, but recorded up to c. 1000 m.

**Food and Feeding.** Chiefly fruit, with a few small animals. Feeds mainly in forest canopy, but also descends to ground.

**Breeding.** Little known. Lays in Jan-Mar; young being fed in nest-hole in early May, in Thailand. Nest in natural cavity or old woodpecker hole, at least 18-21 m up in tall forest tree. Clutch 1-3 eggs; no information on incubation and fledging periods.

**Movements.** None known; previous reports of large flocks and roosts, suggesting extensive local movements in search of fruiting trees, but possible confusion with *R. undulatus*.

**Status and Conservation.** VULNERABLE. CITES I & II. Uncommon to rare throughout limited range. Status uncertain in Myanmar, where said to have been formerly abundant; no recent reports of large flocks. Thailand reckoned to hold under 1000 individuals, but one roost recently discovered with c. 900 individuals, implying overall total probably somewhat higher than previously thought. Generally wary, and difficult to separate in the field from *R. undulatus*, making assessment of status more problematic; frequent reports over many years of large flocks of several thousand birds in N Peninsular Malaysia, however, recently confirmed as referring to this species, and it may be commoner in S of range than previously thought; old records from India, N Myanmar and Sumatra probably erroneous, due to confusion with *R. undulatus*. Main threat is rampant deforestation of lowlands throughout its range; hunting also significant, especially in Myanmar and Thailand, and effects made more serious due to species' gregarious habits; some collecting for wild-bird trade. Occurs in Kaeng Krachan and Khao Laem National Parks and Huai Kha Khaeng Wildlife Sanctuary, in Thailand. Further study required to evaluate this hornbill's true status and the limits of its range.

**Bibliography.** Anderson (1887), Andrew (1992), Chimchome *et al.* (1998), Collar & Andrew (1988), Collar *et al.* (1994), Deignan (1945), Elbel (1969, 1977), Grimmett *et al.* (1998), Ho Huachew & Supari (1997, 2000), Inskipp *et al.* (1996), Kazmierczak (2000), Kemp (1979, 1988), Lekagul & Round (1991), MacKinnon & Philipps (1993), van Marle & Voous (1988), Ng Beechoo (1998), Oates (1883), Poonswad (1993b), Rasmussen (2000), Riley (1938), Robson (2000a, 2000b), Round (1985, 1988), Sanft (1953), Smythies (1986), Stattersfield & Capper (2000), Wells (1999).

## 46. Wreathed Hornbill

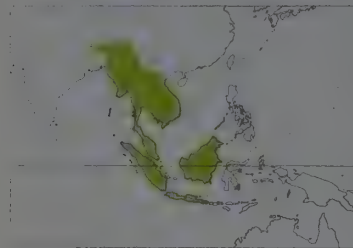
*Rhyticeros undulatus*

**French:** Calao festonné **German:** Furchenhornvogel **Spanish:** Cálao Gorginegro  
**Other common names:** Bar-pouched/Bar-throated Wreathed Hornbill, Northern Waved Hornbill

**Taxonomy.** *Buceros undulatus* Shaw, 1811, Java.

Genus sometimes merged with *Aceros*. Has in past sometimes been treated as conspecific with *R. subruficollis*. N mainland population described as race *ticehursti* on basis of larger size, and smaller Bornean birds as *aequalis*, but variation apparently clinal and racial separation unwarranted. Monotypic.

**Distribution.** S Bhutan and NE India E to Vietnam (N Annam), and S to Sumatra, Borneo, Java and Bali, including several intervening offshore islands.



**Descriptive notes.** 75–85 cm; male 1680–3650 g, female 1360–2685 g. Large, black hornbill with short white tail. Male has crown and nape dark red-brown, head and neck to upper breast creamy white; bill pale yellow, basal half of both mandibles with prominent orange-brown ridges; low wreathed casque brownish and yellow; bare skin around eye pinkish-red; inflatable throat skin yellow with blue-black central bar. Distinguished from *R. subruficollis* by larger size, dark bar across throat sac, ridged mandibles. Female smaller, head to breast all black, throat sac blue with darker band. Juvenile similar to adult male,

but smaller bill, no casque.

**Habitat.** Extensive tracts of primary evergreen forest, mainly among foothills but up to 2560 m; extends into selectively logged areas and coastal forest.

**Food and Feeding.** Mainly fruit; also small animals, especially when breeding. Fruits of at least 30 plant genera recorded; proportions of figs and lipid-rich drupes eaten vary according to locality and season. Animal food generally less than 5% of diet, includes contents of bird nests, reptiles, snails, insects, centipedes, millipedes and crabs. Forages mainly in canopy; descends to ground for fallen fruit and to take animals, especially during midday rest period.

**Breeding.** Lays in Apr-Jun in India, in Jan-Mar elsewhere, extending to Jun-Sept in Borneo and Java. Nest in natural hole 18–28 m up in tree, often *Dipterocarpus* or *Syzygium* species; same cavity often used in successive seasons; female seals nest entrance with droppings. Clutch usually 2 eggs (1–3), but only 1 chick ever raised; incubation c. 40 days; chick with pink skin that soon turns black; male feeds female and chick in nest by regurgitation, up to 120 fruits per visit; female emerges from nest when chick fledges, does not always moult remiges and rectrices together while breeding; fledging 90 days; whole nesting cycle 111–137 days; juvenile remains with parents for several months after leaving nest.

**Movements.** No regular movements, but ranges widely in search of fruiting trees, even crossing between islands, such as Java and Bali, and up to 1000 or more birds gather from wide area at communal roosts.

**Status and Conservation.** Not globally threatened, CITES II. Locally common in several areas across its wide range, which includes several large reserves and at least seven national parks, e.g. Khao Yai (Thailand), Ulu Belum and Gunung Mulu (Malaysia) and Bali Barat (Bali). Among more sedentary Thailand population, breeding home range 10 km<sup>2</sup> and non-breeding 28 km<sup>2</sup>. Although still common, has been eliminated from many marginal areas, and distribution now patchy as result of forest loss and species' requirement for large, unbroken tracts of forest. Still hunted in several areas.

**Bibliography.** Ali (1996), Ali & Ripley (1983), Anggraini *et al.* (2000), Assink (1981), Bartels (1956), Bartels & Bartels (1937), Bell & Brunning (1979), Buri (1996), Chak Sokhachicheaboth (1998), Chauilua *et al.* (1998), Datta (1998), Davison (1995), Deignan (1945), Deniel (1958), Duckworth *et al.* (1999), Dunselman (1937), Eames & Robson (1992), Elbel (1977), Frith & Douglas (1978), Ghosh (1994), Grimmett *et al.* (1998), Hiddinga (1996a), Holmes *et al.* (1993), Hoogerwerf (1950a), Inskipp, C. *et al.* (1999), Inskipp, T. *et al.* (1996), Jeyarajasingam &

Pearson (1999), Johns (1987, 1988), Kemp (1979, 1988), Kemp & Kemp (1975a), King & Wiersma (1996), Leighton (1986), Leighton & Leighton (1983), Lekagul & Round (1991), MacKinnon & Philipps (1993, 2000), Madoc (1976), van Marle & Voous (1988), McClure (1970), Medway & Wells (1976), Poonswad (1993b, 1995), Poonswad & Tsuji (1994), Poonswad, Chauilua *et al.* (1998), Poonswad, Chimchome *et al.* (1998), Poonswad, Tsuji & Ngarmpongsai (1983, 1986, 1987, 1988), Riley (1938), Robson (2000a), Round (1985, 1988), de Ruiter (1997), Scheres & Alba (1997), Smythies (1986, 1999), Thewlis *et al.* (1998), Tickell (1864), Tikader (1983), Tsuji *et al.* (1987), Wells (1999), Wilkinson, Dutson & Sheldon (1991).

## 47. Sumba Hornbill

*Rhyticeros everetti*

**French:** Calao de Sumba **German:** Sumbahornvogel **Spanish:** Cálao de la Sumba  
**Other common names:** Sumba Wreathed Hornbill, Everett's Hornbill

**Taxonomy.** *Rhytidoceros everetti* Rothschild, 1897, Sumba.

Genus sometimes merged with *Aceros*. Monotypic.

**Distribution.** Sumba (Lesser Sunda Is).



**Descriptive notes.** 55 cm. Small, black hornbill, long all-black tail distinctive. Male head and neck dark rufous, darker on crown and nape; bill pale yellow, red near base; low wreathed casque yellowish and brown; bare skin around eye blue; throat skin dark blue, darker central patch; eyelids pink. Female smaller, head and neck black. Juvenile resembles adult male, but bill small, no casque.

**Habitat.** Patches of primary deciduous forest, but extends into secondary forest and open parkland with fruiting trees; occurs at up to 950 m.

**Food and Feeding.** Only fruit recorded in diet, especially figs, but probably takes some small animals. Usually in pairs, but up to 15 may gather at fruiting trees. Flies long distances over forest and grassland to reach food.

**Breeding.** Little known. Copulation observed in Sept, probably lays in Oct-Nov. Nest in natural cavity 10–23 m up in large live deciduous tree, especially *Tetrameles*, mostly where a branch has fallen off; once in folds of a strangler fig; nest entrance 18–24 cm deep, 12–40 cm wide; often 1 or 2 parrot nests in other cavities in same tree. No other information.

**Movements.** Irregular local movements between feeding and roosting sites; up to 70 birds may gather at roost.

**Status and Conservation.** VULNERABLE. CITES II. Restricted to single island, on which forest habitat suitable for hornbills has declined by 60%, to c. 1732 km<sup>2</sup> (c. 10% of island's surface area), since 1927. Habitat thus patchy, and of irregular size and distribution; species recorded from 18 out of 33 patches, mostly those over 1000 ha in area. Recent total population estimates of 4000 (maximum 6500) birds, although breeding population may be significantly lower, as a result of general fragmentation of habitat and also delayed maturity of birds before reaching breeding condition. Still locally common in primary forest with tall canopy, large trees and low levels of disturbance, especially in Manupeu-Langgaliru National Park in W Sumba, and occurs also in Laiwangi-Wanggameti National Park in E; these reserves both newly designated, and total 135,000 ha of forest. Scattered large fig trees seem especially important as food, but these and forest margins continually affected by grassland fires, set to improve grazing. Preference for nesting in larger *Tetrameles* trees also restrictive. Still trapped and hunted for food and wild-bird trade to a small degree, and shows low tolerance to human disturbance within forest.

**Bibliography.** Andrew (1992), Anon. (1988, 1995d), Coates & Bishop (1997), Collar & Andrew (1988), Collar *et al.* (1994), Holmes *et al.* (1993), Inskipp *et al.* (1996), Jepson (1994), Jones & Banjaransani (1990), Jones, Juhaeni *et al.* (1994), Jones, Linsley & Marsden (1995), Juhaeni (1993a, 1993b), Kemp (1979, 1988), Kinnaird & O'Brien (1995), Linsley *et al.* (1999), Marsden (1999), Marsden & Jones (1997), O'Brien & Kinnaird (1996a, 1996b), O'Brien *et al.* (1998), Riffel & Dwi (1991), Stattersfield & Capper (2000), Stattersfield *et al.* (1998), Sujatnika & Jepson (1995), White & Bruce (1986).







49



51

50

52

PLATE 43

inches 6  
cm 16



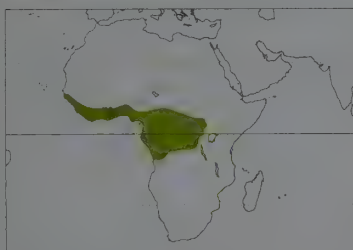
# Genus *BYCANISTES* Cabanis and Heine, 1860

## 48. Piping Hornbill

### *Bycanistes fistulator*

**French:** Calao siffleur **German:** Schreihornvogel **Spanish:** Cálao Silbador  
**Other common names:** Laughing/Whistling/White-tailed Hornbill

**Taxonomy.** *Buceros Fistulator* Cassin, 1850, St Paul's River, Liberia. Genus sometimes merged with *Ceratogymna*. Race *sharpii* intergrades with nominate along R Niger, and with *duboisii* in E Cameroon. Three subspecies recognized.  
**Subspecies and Distribution.**  
*B. f. fistulator* (Cassin, 1850) - Senegal E to W Nigeria (E to R Niger).  
*B. f. sharpii* (Elliot, 1873) - R Niger E to S Chad, S to NW Angola and W Zaire.  
*B. f. duboisii* W. L. Sclater, 1922 - Central African Republic and Congo Basin E to S Sudan and W Uganda, S to SC & E Zaire.



**Descriptive notes.** 45 cm; male 463-710 g, female 413-500 g. Medium-smallish pied hornbill with white belly and rump. Male nominate race wings black, central secondaries broadly white-tipped, white tips to outer tail; bill and casque ridged, brownish, bill base creamy; bare skin around eye dark blue. Female smaller, bill and casque smaller, bill base darker. Juvenile similar to adult, but bill small with no casque, brown feathers around base. Race *sharpii* larger, white on inner primaries and all secondaries, outer tail all white, bill creamy with darker central patch, bill and casque unridged; *duboisii* similar but even

larger, outer primaries also with broad white tips, casque bigger.  
**Habitat.** Primary evergreen forest and surrounding gallery forest, mangrove forest and swamp-forest, also secondary forest and plantations; lowlands up to 600 m.  
**Food and Feeding.** About 90% of diet fruit, from at least 40 plant genera and 12 families; also, few insects. Usually forages 30-50 m up in forest canopy; sometimes flies out to hawk insects, or descends to follow driver-ants. Generally in family groups, or in small flocks (up to 37 birds recorded in a flock).

**Breeding.** Little known. Probably lays aseasonally, in Jan. Apr, Jun and Oct-Dec in W Africa, and in Jan-Feb, Apr, Jul and Sept-Dec in C & E Africa. Nest in natural cavity 8-15 m up in tree. Clutch 1-3 eggs, but usually only 1 chick reared; female may not always moult remiges and rectrices when breeding; no information on other aspects of breeding.

**Movements.** Generally considered sedentary; no regular fluctuations in numbers, but some movements in Liberia, and in some years may appear far from usual range. On a local scale, flies long distances between fruiting trees and to communal roosts.

**Status and Conservation.** Not globally threatened. Generally common across wide range, and occurs in most large forest reserves. Occupies, and often common in, secondary and agricultural stands of tall trees alongside primary forest. Seems to be important agent in dispersal of seeds of several tree and liana species.

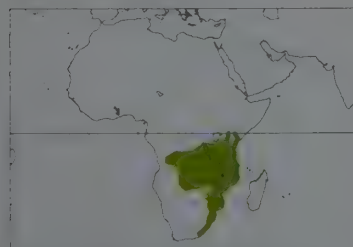
**Bibliography.** Bannerman (1953), Barlow *et al.* (1997), Breitwisch (1983), Britton (1980), Brosset & Éard (1986), Chapin (1939), Cheke & Walsh (1996), Christy & Clarke (1994), Colston & Curry-Lindahl (1986), Dean (1973, 2000), Dowsett & Dowsett-Lemaire (1991, 1993, 1997), Dowsett & Forbes-Watson (1993), Dutson & Branscombe (1990), Elgood *et al.* (1994), Field (1999), Fry *et al.* (1988), Gartshore (1989), Gartshore *et al.* (1995), Gatter (1997), Germain *et al.* (1973), Grant & Mackworth-Praed (1946), Green & Carroll (1991), Grimes (1987), Kemp (1976a), Kemp & Crowe (1985), Lamarque (1980), Lippens & Wille (1976), Louette (1981b), Mackworth-Praed & Grant (1957, 1962, 1970), Marchant (1953), Marin & Matesanz (1999), Morel & Morel (1990), Pinto (1983), Serle (1957), Short *et al.* (1990), Snow (1978), van Someren (1949), Thomas (1991), Whitney & Smith (1998), Whitney *et al.* (1998), Willis (1983).

## 49. Trumpeter Hornbill

### *Bycanistes bucinator*

**French:** Calao trompette **German:** Trompeterhornvogel **Spanish:** Cálao Trompetero

**Taxonomy.** *Buceros bucinator* [sic] Temminck, 1824, Knysna, South Africa. Genus sometimes merged with *Ceratogymna*. Monotypic.  
**Distribution.** N & NE Angola and S Zaire across to S Kenya, and S to NE Namibia, N Botswana, E Zimbabwe and E South Africa.



**Descriptive notes.** 50-55 cm; male 607-941 g, female 452-670 g. Medium-sized black hornbill with white back and belly; white tips to secondaries, inner primaries and tail. Male has bill and casque black, circumorbital skin red to purple. Female smaller, casque much smaller, bill yellow at base and tip. Juvenile similar to adult, but brown-tipped feathers on face and at base of casqueless bill.

**Habitat.** Inhabits gallery, riverine and coastal evergreen forest, extending into tall deciduous woodland and wooded hillsides; occurs at up to 2200 m.

**Food and Feeding.** Main diet a wide variety of at least 14 genera of fruits, especially figs and *Trichelia*; also some small animals, mainly insects, but also small birds and nestlings, crabs, millipedes and woodlice. Forages mainly among foliage, often resting in dense cover near fruiting trees; sometimes takes food in flight.

**Breeding.** Lays in Sept-Jan. Monogamous; sometimes second male or young of previous year in attendance as helper. Nest in natural cavity 2-13 m up in tree or in high rock face, up to 8 km from nearest food; main lining bark and wood flakes; both sexes seal nest, with mud pellets regurgitated by male or carried in bill. Clutch 2-4 eggs, laid at intervals of 2-3 days after pre-laying period 10-15 days; incubation 28 days; chick sizes staggered; male regurgitates up to 38 food items on each feeding visit; female moults remiges and rectrices while nesting, but not always simultaneously, emerges when chicks fledge; fledging at least 50 days; in captivity, whole nesting cycle 88-117 days.

**Movements.** Resident in many areas, but ranges widely in search of fruiting trees, even across dry savanna; a few areas visited regularly only for fruit, or erratically for breeding. Gathers from at least 15 km to communal roosts, of up to 200 birds.

**Status and Conservation.** Not globally threatened. Thinly distributed across wide range, but locally common in many areas. Occurs in Victoria Falls and Zambezi National Park, in Zimbabwe. Able to exist in range of wooded habitat types, including secondary and agricultural areas.

**Bibliography.** Benson & Benson (1977), Benson *et al.* (1971), Britton (1980), Chapin (1939), Clancey (1996), Dean (2000), Dowsett & Dowsett-Lemaire (1993), Dowsett & Forbes-Watson (1993), Dowsett-Lemaire (1988, 1989), Evans & Anderson (1992), Fry *et al.* (1988), Ginn *et al.* (1989), Grant & Mackworth-Praed (1946), Hansen (1992), Harrison *et al.* (1997), Jokumsen (1995), Kemp (1976a), Kemp & Crowe (1985), Lewis (1982), Lewis & Pomeroy (1989), Lippens & Wille (1976), Macdonald (1984), Mackworth-Praed & Grant (1957, 1962, 1970), Maclean (1993), Millar (1921), Onderstall (1989), Penry (1994), Pinto (1983), du Plessis (1994a), Pomeroy & Tengeche (1980), Reinhard & Strehlow (1998), de Ruiter (1995, 1996), Scheres & Alba (1997), Short *et al.* (1990), Snow (1978), Stonor (1936), Vernon (1991), Wilkinson & Merry (1991), Zimmerman *et al.* (1996).

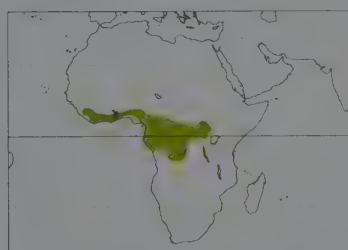
## 50. Brown-cheeked Hornbill

### *Bycanistes cylindricus*

**French:** Calao à joues brunes **German:** Braunwangen-Hornvogel **Spanish:** Cálao Caripardo  
**Other common names:** White-thighed Hornbill (*albotibialis*)

**Taxonomy.** *Buceros cylindricus* Temminck, 1831, Cape Coast, West Africa. Genus sometimes merged with *Ceratogymna*. Distinctive race *albotibialis*, with discrete range, possibly a separate species. Two subspecies recognized.

**Subspecies and Distribution.**  
*B. c. cylindricus* (Temminck, 1831) - Sierra Leone E to Togo.  
*B. c. albotibialis* (Cabanis & Reichenow, 1877) - Benin E to W Uganda and S to Congo, W Zaire and N Angola.



**Descriptive notes.** 60-70 cm; male 1200-1411 g, female 908-1043 g. Medium-sized to large black hornbill with white rump, tail-coverts and belly, broad white trailing edge to wings, white tail with broad black band across centre. Male of nominate race has brown-tipped feathers on face; bill and high tubular casque cream-coloured, base of lower mandible grooved, casque with grooves at sides and wrinkles at base; circumorbital skin red, eyes dark red. Female smaller, much smaller bill and casque blackish, circumorbital skin pink to cream. Juvenile like adult, but smaller bill without casque. Race *albotibialis* has white thighs, face

without brown feather tips, male bill less grooved, dark brown with creamy base and tip, casque longer and laterally flattened, more projecting at front, only slightly grooved, circumorbital skin pale yellow, eyes browner.

**Habitat.** Extensive stands of tall lowland evergreen forest, less often in adjacent secondary forest, and even in plantations; recorded rarely up to 4054 m.

**Food and Feeding.** About 90% of diet fruit, from at least 38 plant genera and 18 families; also a few insects, and bird eggs and nestlings. Most often forages 25-50 m up in canopy of large emergent or isolated trees, but sometimes descends into secondary growth or flies out to hawk insects. Usually in pairs or small groups, rarely as many as 90 gathering in fruiting tree.

**Breeding.** Little known. Probably lays mainly in Sept-Nov in Liberia, when males can be seen alone; more aseasonally elsewhere, in Jan-Apr, Jun-Aug and Oct-Dec; appears not to breed every year. Nest in natural cavity 20-25 m up in tree. Clutch size not known; 2 nestlings recorded, but often only single fledged chick with parents; male feeds female in nest by regurgitation, at least 12 fruits per visit and 14-18 visits per day. No information available on incubation and fledging periods.

**Movements.** Local populations fluctuate 12-fold and in synchrony in Cameroon, suggesting regional movements to track fruit availability; once wandered high up on Mt Cameroon. Previously described as more sedentary in Gabon, but as nomadic during non-breeding season in Liberia, in flocks of up to 50, and in Uganda.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Few data on numbers; 2 nests recorded 2-4 km apart, and 2 pairs occupied 300 ha of forest. Nominate race uncommon, and has declined in several areas in W Africa; if races prove to be distinct species, nominate would then occupy a restricted range which has been much altered by deforestation. Forest destruction and fragmentation appear to be main threats. Generally absent from Dahomey Gap. Always the first large hornbill species in an area to be affected by forest disturbance, although also occurs in disturbed areas and even plantations. Occurs in Maraué National Park and is widespread and common in Tai Forest National Park, in Ivory Coast. Race *albotibialis* commoner over its more extensive range, and regularly uses secondary forest habitats. Species appears to be important in dispersal of seeds of several forest trees and lianas.

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## 51. Grey-cheeked Hornbill

*Bycanistes subcylindricus*

**French:** Calao à joues grises **German:** Grauwangen-Hornvogel **Spanish:** Cálao Carigrís  
**Other common names:** Black-and-white-casqued Hornbill

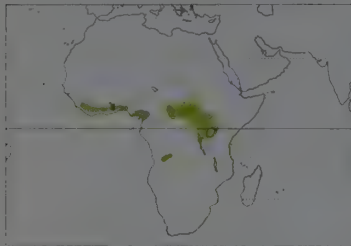
**Taxonomy.** *Buceros subcylindricus* P. L. Selater, 1870, Ashanti, Ghana.

Genus sometimes merged with *Ceratogymna*. Races rather poorly differentiated. Two subspecies currently recognized.

**Subspecies and Distribution.**

*B. s. subcylindricus* (P. L. Selater, 1870) - Sierra Leone, NE Liberia and Ivory Coast E to W Nigeria (delta of R Niger).

*B. s. subquadratus* Cabanis, 1880 - E Nigeria, Cameroon and Central African Republic E to S Sudan, and S to N & E Zaire, Uganda, SW Kenya and NW Tanzania; also N Angola.



**Descriptive notes.** 60-70 cm; male 1078-1525 g, female 1000-1250 g. Medium-sized to large black hornbill with white rump, tail-coverts and belly, broad white trailing edge to wings (including even tips of greater coverts), white-tipped outer tail feathers, grey-tipped feathers on face. Male nominate race bill dark brown; high ridged casque broad at base, laterally flattened with anterior projection, sides wrinkled, dark brown, creamy base; circumorbital skin flesh-coloured. Female smaller, bill and casque blackish. Juvenile bill small, no casque. Race *subquadratus* larger, more white below, rear half of casque creamy.

**Habitat.** Ecotone between evergreen forest, or forest patches, and secondary forest, also tall deciduous woodland and plantations, at up to 2600 m.

**Food and Feeding.** Mainly fruit, from at least 41 plant genera, and especially figs; also small animals, mainly insects, but including millipedes, snails, lizards, bats, nest contents of birds, and small galagos. Feeds mainly in canopy, picking off fruit. Readily takes any small animals, extracted from vegetation, snatched in flight, or picked from the ground; sometimes hunts in groups. Often associates with monkeys and squirrels.

**Breeding.** Probably aseasonal, lays in Jan-May in C Africa, mainly Aug-Mar in E Africa. Monogamous in pairs. Nest in natural cavity 9-30 m up in tree or, less often, on rock face; both sexes seal nest entrance, mainly with mud pellets provided by male. Clutch 2 eggs; incubation 42 days; chick skin pink at hatching, soon turning dark grey; male feeds female in nest by regurgitation, up to 200 fruits per visit; female may not always moult remiges and rectrices together when breeding; usually only 1 chick reared, second-hatched dying of starvation; fledging 70-79 days.

**Movements.** Ranges locally in search of fruiting trees, but usually in pairs; only occasionally larger flocks and roosts.

**Status and Conservation.** Not globally threatened. Local and uncommon in much of W Africa and Angola, but more common in some parts; still common in C & E Africa, especially along R Congo. Occurs in Kibira National Park, in Burundi, and in Impenetrable (Bwindi) Forest National Park, in Uganda. Its preference for ecotones ameliorates some of the effects of forest degradation, but leads to patchy distribution; however, species may expand range around areas of cleared forest in W Africa, but then rapidly becomes vulnerable to hunting in these areas.

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(1989), Lippens & Wille (1976), Louette (1981b), Mackworth-Præd & Grant (1957, 1962, 1970), Moreau & Moreau (1937), Morel & Morel (1990), Nikolaus (1987), North (1942), Pinto (1983), Pitman (1928, 1974), Porritt & Riley (1976), Prigogine (1980), Reinhard & Strehlow (1998), Short *et al.* (1990), Snow (1978), Zimmerman (1972), Zimmerman *et al.* (1996).

## 52. Silvery-cheeked Hornbill

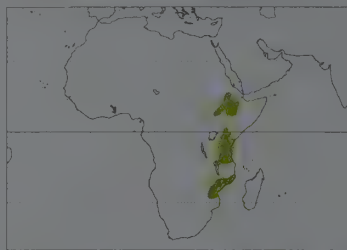
*Bycanistes brevis*

**French:** Calao à joues argent **German:** Silberwangen-Hornvogel **Spanish:** Cálao Cariplatado

**Taxonomy.** *Bycanistes cristatus brevis* Friedmann, 1929, Usambara Mountains, Tanzania.

Genus sometimes merged with *Ceratogymna*. In past, N populations sometimes separated as race *omissus*. Monotypic.

**Distribution.** Ethiopian Highlands, SE Sudan and C Kenya S to E & S Tanzania and Malawi; and C Mozambique to SE Zimbabwe.



**Descriptive notes.** 60-70 cm; male 1265-1400 g, female 1050-1450 g. Medium-sized to large black hornbill with noticeable silvery-grey feathering on face; white back, rump and tail-coverts, broad white tips to outer tail feathers, and yellowish line across base of dark brown bill. Male has casque large and curved, cream-coloured; circumorbital skin blue-black. Female smaller than male, with casque smaller and darker; pink circumorbital skin. Juvenile without whitish facial feathers, bill small, lacks casque.

**Habitat.** Inhabits montane and coastal evergreen forest, extending to gallery, riverine and

tall deciduous forest and woodland; occurs at up to 2600 m.

**Food and Feeding.** Mainly fruit, from at least 26 plant genera, especially cherry-sized drupes and figs; some small animals, mainly insects, but also spiders, centipedes, lizards, and birds and nest contents. Forages mainly among foliage, but some food taken on the wing; sometimes descends to ground to feed. Rarely, drinks water.

**Breeding.** Lays in Feb-Jul in Ethiopia, in Oct-Nov in Kenya, and in Aug-Nov in Tanzania and farther S. Monogamous in pairs. Nest in natural cavity 7-25 m up in large tree; both sexes seal nest entrance with mud pellets formed by male. Clutch 1-2 eggs; incubation 40 days; chick skin changes from pink to dark grey within few days of hatching; male feeds female with fruits regurgitated at nest, up to 69 fruits per visit and up to 24 visits daily, estimated 24,000 fruits delivered in total of 1600 visits over entire nesting cycle; female remains in nest until chick fledges, usually moults all remiges and rectrices together; fledging 77-80 days; whole nesting cycle 107-138 days.

**Movements.** Makes long flights in search of fruiting trees, including from communal roosts of up to 200 birds, often with *B. bucinator*. Nomadic flocks form mainly in dry non-breeding season. Recorded as vagrant in NE Zambia and NE South Africa.

**Status and Conservation.** Not globally threatened. Locally common, but with patchy distribution, and erratic occurrence in marginal habitats and during droughts. Locally vulnerable to deforestation, but does use variety of habitats, and able to move about in search of food and nesting sites.

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53



54

PLATE 44

inches 6  
cm 15

## PLATE 44

## Family BUCEROTIDAE (HORNBILL) SPECIES ACCOUNTS

### Genus *CERATOGYMNA* Bonaparte, 1854

#### 53. Black-casqued Hornbill

##### *Ceratogymna atrata*

**French:** Calao à casque noir **German:** Schwarzhelm-Hornvogel **Spanish:** Cálao Casquinegro  
**Other common names:** Black-casqued Wattled Hornbill

**Taxonomy.** *Bucerns atratus* Temminck, 1835, Ashanti, Ghana.  
Monotypic.

**Distribution.** S Guinea and Sierra Leone E to S Sudan and W Uganda, and S to NW Angola and S Zaire; also Bioko I (Fernando Pôo).

**Descriptive notes.** 60-70 cm; male 1069-1600 g, female 907-1182 g. Large black hornbill with white only on tips of outer tail feathers. Male has head to breast deep black; distinctive blue pendulous throat wattles are not inflatable; bill and huge cylindrical casque black; circumorbital skin and inflatable throat skin blue; eyes red. Female smaller than male; has head and neck rufous, bill and much smaller casque horn-coloured, wattles smaller, eyes brown. Juvenile resembles adult female, but bill small and lacks casque.

**Habitat.** Inhabits lowland evergreen forest, mainly in primary tracts, but often extending

into adjacent secondary and gallery forest, also plantations; occurs at up to 1500 m.

**Food and Feeding.** About 90% of diet fruit, of at least 37 plant genera and 20 families, including figs and, especially, oil palms (*Elaeis guineensis*); eats some small animals, especially insects, and also seen raiding nests of weavers (*Ploceus*). Forages mainly in canopy, but descends to ground for seeds and insects; even hawks insects above canopy. Recorded several times to drink water, more often than any other hornbill.

**Breeding.** Little known. Probably aseasonal, lays about Dec-Feb in Liberia, in Jul-Sept in rest of W Africa, and in Apr, Jun-Jul and Oct-Dec in C & E Africa; appears not to breed every year. Possibly co-operative, in groups of up to 5, with more females and juveniles than adult males. Clutch 1-2 eggs, but usually only single fledged chick seen with parents. Nest in natural cavity 10-23 m up in tree; both sexes seal nest entrance, with mud pellets formed by male. Incubation and fledging periods not documented.

**Movements.** Wanders extensively, over at least 100 km, in search of fruiting trees, but exact movements unknown. Occurs as families or in flocks of up to 40 birds, but local 4-fold fluctuations in numbers, in synchrony in adjacent areas of Cameroon, and cohesive movements in Liberia, suggest tracking of fruit availability. Wandering birds roost communally, 5-8 m up in swamp vegetation or, more often, 20-50 m up in canopy.

**Status and Conservation.** Not globally threatened. Common at only few localities in W Africa, and eliminated from many areas by habitat alteration and hunting; more common and widespread in C & E Africa. Occurs in several protected areas, e.g. Marauoué and Tai Forest National Parks (Ivory Coast) Dja National Park (Cameroon) and La Lopé National Park (Gabon). Prefers mature forest, so vulnerable because of its large size, low natural population density, and fragmentation of forest tracts. Appears to be important agent in dispersal of seeds of several forest trees and lianas.

**Bibliography.** Bannerman (1953), Basilio (1963), Brosset & Énard (1986), Cave & Macdonald (1955), Chapin (1939), Cheke & Walsh (1996), Christy & Clarke (1994), Colston & Curry-Lindahl (1986), Dean (2000), Dowsett & Dowsett-Lemaire (1991, 1993, 1997), Dowsett & Forbes-Watson (1993), Dutson & Branscombe (1990), Elgood *et al.* (1994), Field (1999), Friedmann & Williams (1971), Fry *et al.* (1988), Gartshore (1989), Gartshore *et al.* (1995), Gatter (1997), Germain *et al.* (1973), Grimes (1987), Halleux (1994), Heinrich (1958), Keith (1969), Kemp (1976a), Kemp & Crowe (1985), Lamperti *et al.* (1996), Lippens & Wille (1976), Louette (1981b), Mackworth-Præd & Grant (1957, 1962, 1970), Nikolaus (1987), Pérez-del Val (1996), Pinto (1983), Poulsen (1970), Prigogine (1971), Serle (1957), Short *et al.* (1990), Smith *et al.* (1993), Snow (1978), Thomas (1991), Whitney & Smith (1998), Whitney, Fogiel, Lamperti *et al.* (1998), Whitney, Fogiel, Smith *et al.* (1996).



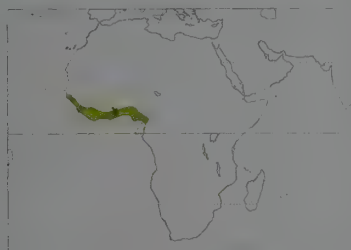
## 54. Yellow-casqued Hornbill

### *Ceratogymna elata*

**French:** Calao à casque jaune    **German:** Goldhelm-Hornvogel    **Spanish:** Calao Casquigualdo  
**Other common names:** Yellow-casqued Wattled Hornbill

**Taxonomy.** *Buceros elatus* Temminck, 1831, Ghana.  
Monotypic.

**Distribution.** S Senegal E to SW Cameroon.



resembles adult female, but bill small and casqueless.

**Descriptive notes.** 60-70 cm; male 2100 g; female 1500-2000 g. Distinctive, large, black hornbill with white outer tail feathers, scaly neck pattern. Male has crown and rear of head black, neck feathers with white bases and brown tips, appearing spotted; bare blue pendulous throat wattles are not inflatable; bill dark grey, high cowl-like yellowish casque with dark base, grooves where bill and casque join; circumorbital and inflatable throat skin blue; eyes red. Female smaller than male, has crown and rear of head rufous, bill and much smaller casque yellow-brown, wattles smaller, neck spotted rufous, eyes brown. Juvenile re-

**Habitat.** Primary lowland evergreen forest, especially along edges of swamps, often extending into secondary, gallery and riverine forest or among plantations, at up to 1000 m.

**Food and Feeding.** Mainly fruit, especially from oil palms (*Elaeis guineensis*), but also other palms; eats insects and millipedes when those available. Forages mainly in forest canopy, at 20-50 m, but some fruit and insects taken from the ground or in flight. Usually in pairs or in small groups of up to 12 birds, often with *Bvcanistes cylindricus*.

**Breeding.** Little known. Probably lays in Sept-Mar, when lone males seen, to coincide with start of fruiting of oil palm. Nest in natural cavity in tall forest tree; pair seen visiting cavity 35 m up. No information on clutch size, incubation and fledging periods, or other aspects of breeding.

**Movements.** Ranges widely in search of fruiting trees; wanderers known to roost communally, with up to 50 birds, sometimes as low down as 3-7 m in swamp vegetation.

**Status and Conservation.** Not globally threatened. Currently considered Near-threatened. Locally common in a few large reserves. Still not uncommon in Nigeria, where population has declined notably due to destruction of forest. Known to have declined in some areas, and to have been eliminated by hunting at several localities, and this remains the main threat. Restricted range for such a large, low-density forest hornbill, and much habitat already lost or degraded within that range. Shows some tolerance of secondary forest and plantations, but particularly vulnerable to hunting in these habitats. Occurs in Basse Casamance National Park (Senegal), Fai Forest National Park (Ivory Coast), and Korup National Park (Cameroon).

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## SUMMARY OF VOLUME 6

COLIIDAE (Mousebirds)  
TROGONIDAE (Trogons)  
ALCEDINIDAE (Kingfishers)  
TODIDAE (Todies)  
MOMOTIDAE (Motmots)  
MEROPIDAE (Bee-eaters)  
CORACIIDAE (Rollers)  
BRACHYPTERACIIDAE (Ground-rollers)  
LEPTOSOMIDAE (Cuckoo-roller)  
UPUPIDAE (Hoopoe)  
PHOENICULIDAE (Woodhoopoes)  
BUCEROTIDAE (Hornbills)

## TECHNICAL DETAILS

- 310 × 240 mm
- 589 pages
- 45 colour plates
- 385 photographs
- 270 distribution maps
- 11 figures and tables
- c. 6000 bibliographical references

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ISBN 84-87334-30-X



9 788487 334306